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PhD thesis

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Plant Community Ecology of a Major Subtropical
Riverine Floodplain

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the Division of Environmental and Evolutionary Biology,
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Abstract

Porto Primavera dam and Itaipu reservoir now form the boundaries of the last remaining stretch of floodplain wetlands on the Rio Paraná in southern Brazil. The construction of numerous hydroelectric schemes on the Paraná has resulted in the submergence of former wetland habitats by reservoirs. Remaining stretches have been degraded by disruption of the natural annual flood pulse, which plays a primary role in the ecological functioning of the floodplain. The floodplain environments forming the subject of this study are of major conservation importance because; i) they are unique, ii) they support a particularly high diversity of many groups of organisms including approximately 176 fish species (many of which are endemic), 351 bird species and over 800 plant species, iii) the pressures from river regulation and other smaller scale human activities (such as sand extraction in the Paraná channel, burning within the floodplain and overfishing) continue to threaten their survival and iv) they have potential as an economic resource in a relatively poor area of Paraná state. This importance has been recognized at state and national levels and three conservation units now span the area; the Environmental Protection Area of the Islands and Várzeas of the River Paraná, Ivinheima River State Park and Ilha Grande National Park.

This project described the vegetation of a stretch of the Paraná River and investigated which natural or human-imposed factors might be controlling its characteristics, its capacity for biodiversity support and its potential to provide an economic resource. This information is of value in the planning of management strategies aiming to conserve biodiversity and develop sustainable ways in which the floodplain resources can be utilised.

Central to this study were the surveys of vegetation and environmental characteristics of aquatic, terrestrial and transitional habitats of the Paraná floodplain near Porto Rico. These produced extensive data sets which helped to reveal the types of vegetation-environment relationships structuring the floodplain plant communities. To complement this investigative approach, three aspects of the functioning of floodplain vegetation were chosen for closer study. These were the impacts of livestock grazing on wetland and island vegetation, competitive interactions between pairs of free-floating aquatic plant species and the role of aquatic macrophytes in contributing carbon to aquatic food webs.

Three major community types were identified in the aquatic habitats of the floodplain, one which included *Eichhornia azurea* in mixture with several free-floating and emergent

species, a second in which *E. azurea* was strongly dominant and a third comprised purely of submerged species. Two strongly contrasting broad vegetation communities were identified at bank and shore environments. *Polygonum* and *Ludwigia* species were important in one group and Poaceae, creepers, woody plants and ferns in the other group. Sub-groups of these communities could also be suggested, but these are less distinct. Most of the floodplain sites supported a Poaceae-creeper community type with the remaining sites supporting a community indicated by *Polygonum* species. The Poaceae group was comprised of a number of sub-communities in which the importance of Poaceae relative to other species varied.

The aquatic vegetation communities differed structurally with contrasting community biomass, canopy height, canopy cover, species richness and stem density. They were associated with waterbodies with different water depth and pH and different sediment nitrogen and phosphorus contents. Water flow rate category and underwater light availability also differed between the sites that tended to support the different vegetation types. The two major bank and shore vegetation communities differed in canopy cover, in the soil nitrogen, phosphorus and calcium levels with which they were associated and in the steepness of the bank on which they tended to grow. Floodplain vegetation communities contrasted in species richness and differed in the soil nitrogen and calcium levels and river systems with which they were associated.

Aquatic species richness was best predicted by a combination of sediment calcium content and canopy height and cover while biomass was best predicted by the proportion of the water column sufficiently illuminated for plant growth. A small amount of variation in canopy height was explained by water conductivity, and like canopy cover and stem density, canopy height was also related to other vegetation variables. There were reasonably strong relationships between bank and shore species richness and soil nitrogen and phosphorus levels. The variation in the remaining collective vegetation variables was not explained by environmental variables although there were relationships with dominant species trait variables and other collective vegetation variables. Some of the variation in floodplain species richness was explained by soil nitrogen while biomass and canopy cover were well predicted by other collective vegetation and dominant species trait variables. Stem density was related to four environmental variables but was best predicted by a combination of distance from the water's edge, canopy cover and the leaf weight of the dominant species.

Investigation of livestock grazing, one of the pressures on the non-aquatic vegetation in the floodplain, showed that some areas of natural vegetation could recover quickly from a single event of biomass removal (cutting treatments). Experiments using 1m² exclosures on a riverine island showed that vegetation previously intensively grazed by cattle quickly increased in canopy height and biomass once protected from grazing, with the additional effects of increased species richness, reduced bare ground and increased biomass of potentially more palatable graminoid species.

Competition experiments conducted on pairs of floating aquatic plant species showed that the effect of interactions depended on the particular combination of species and was influenced by nutrient availability. *Pistia stratiotes* was found to be aggressive towards *Limnobium laevigatum*, but when *Pistia* interacted with *Salvinia auriculata*, there was little effect on either species. Although *Limnobium* appeared to be of low competitive ability when interacting with *Pistia*, it slightly suppressed the growth of *Salvinia* in fertilised treatments. In addition, *Pistia* and *Limnobium* both showed a response to increased nutrient availability of increased production of low biomass daughter plants. Future changes in nutrient availability in floodplain waterbodies caused by river regulation can be expected to affect competitive interactions between free-floating aquatic macrophytes.

Analysis of carbon stable isotopes of aquatic macrophytes showed contrasting signatures between plants with different photosynthetic strategies and/or utilising different sources of carbon. The attempt to trace macrophyte-derived carbon into sediment underlying plant stands and into invertebrate consumers was not successful. Much further work is required to uncover the pathway by which macrophyte derived carbon is cycled through food webs.

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Author's Declaration

I declare that the work described in this thesis has been carried out by myself, except where otherwise acknowledged. It is entirely of my own composition and has not, in whole or in part, been submitted for any other degree.

Judith Milne

A handwritten signature in cursive script, appearing to read 'Judith Milne', written in black ink.

June 2004

1 Introduction

1.1 Project outline

The last remaining stretch of floodplain wetlands of the Upper Paraná River in Brazil is an area threatened by encroaching large-scale hydroelectric schemes and vulnerable to smaller-scale local exploitation. The Paraná is a major river with a total drainage area of 2.8 million square kilometres. This natural resource provides an opportunity for power generation in Brazil, a country lacking in fossil fuel resources. As a result, the river is now regulated by a series of more than 130 dams greater than ten metres high. Such regulation can have numerous effects on the character and functioning of a river and on the plants and animals that it supports (Cairns 1995; Petts 1984; Petts 1996; Ward & Stanford 1995). The patchwork of wetlands, lagoons, flowing channels and forested islands in the floodplain provides diverse habitats (Junk, Bayley & Sparks 1989). These support large numbers of various groups of animals, including 176 species of fish (Agostinho, Thomaz & Gomes 2004 in press), many of which utilise the floodplain for feeding, breeding and shelter while young (Agostinho & Zalewski 1995).

An immediate effect of dam construction in the Paraná River has been the flooding of upstream floodplains, wiping out vegetation and habitats vital for biodiversity support functions, including fish reproduction. Prior to the completion of Porto Primavera dam in 1998, 40 kilometres upstream of the town of Porto Rico, the last remnant of semi-natural floodplain vegetation associated with the Brazilian Paraná stretched 480 kilometres from Três Lagoas city in the state of Mato Grosso do Sul to Guaira in Paraná state. Porto Primavera dam has flooded the upstream half of this stretch (Figure 1.1) leaving only 230 kilometres of floodplain free from dams, although with a hydrologic regime highly regulated by the upstream dams (Agostinho *et al.* 2000).

The main effect of regulation of the Paraná River has been a reduction in the amplitude of annual variation in water level by the retention of water behind dams to allow reservoirs to fill during the wet season and the release of water during the dry season (Agostinho *et al.* 2000). Following the completion of Porto Primavera dam, floodwaters were retained in the reservoir to allow it to fill for the first time, resulting in reduced river flow through the floodplain. Differences in aquatic community structure and limnological characteristics have been found between years in which floods naturally did or did not occur (Agostinho

et al. 2000). Water levels also affect the distribution and abundance of wetland and aquatic plant species which have limited tolerances of water depth.



Figure 1.1 Inundation of the Paraná River floodplain upstream of Porto Primavera dam.

In parallel with the large-scale changes seen over time due to dam construction, local-scale human impacts also influence the ecology of the floodplain. Since the modern phase of colonisation of the north of Paraná state, which began in the 1930s, people have been causing major changes to the appearance and functioning of the Paraná floodplain near Porto Rico. Before this colonisation, the islands and dry parts of the floodplain were covered by extensive riparian forest, of which only fragments now remain (Campos 1999a). Deforestation was driven by the timber industry and by the need for farmland. The floodplain supported the settlers who lived off the natural fishery and cleared the forest to use the land for small-scale cropping. However, damage to the floodplain vegetation, disruption of the natural river flow regime and over-fishing have led to the current situation in which professional fishermen are banned from fishing during the fish breeding season and instead are paid compensation by the government. Subsistence crop farming is seen occasionally but cattle grazing appears to be the main use made of the drier floodplain areas. The cattle have caused major changes to the vegetation through intense grazing pressure on palatable species and trampling, which exposes bare ground to erosion. Farming and fishing processes have been detrimental to the integrity of the floodplain which can no longer support these activities as well as it once did (Agostinho, Thomaz &

Nakatani 2002). This has been recognized by the Brazilian authorities and three levels of environmental protection currently apply to certain areas of the Paraná floodplain (Table 1.1, Figure 1.2). However, the need for resources, ranging from electricity to small patches of land for subsistence farming, persists and so the floodplain continues to be vulnerable to human pressures. Understanding how this environment functions is therefore vital for determining its sustainability over time.

Table 1.1 Legal protection of the floodplain of the Upper Paraná River

Level of protection	Conservation unit	Area km ²
Local	Area of Environmental Protection of the Islands and Várzeas of the Paraná River	10 031
State	Ivinheima River State Park	700
National	Ilha Grande National Park	778

The floodplain environment supports a wealth of plant and animal groups, many of which have been little studied, including the floodplain vegetation which forms the centre of this study. It has also been seen in the past that the floodplain can support a human population to a certain degree through farming and fishing. However, degradation of the rich habitats has eroded both of these functions previously performed by the floodplain. The aim of this work is to describe the vegetation which plays roles in floodplain functioning, biodiversity support and provision of an economic resource to the local population, and to identify factors which regulate it, thus contributing to the knowledge base needed to make appropriate management decisions for the floodplain.

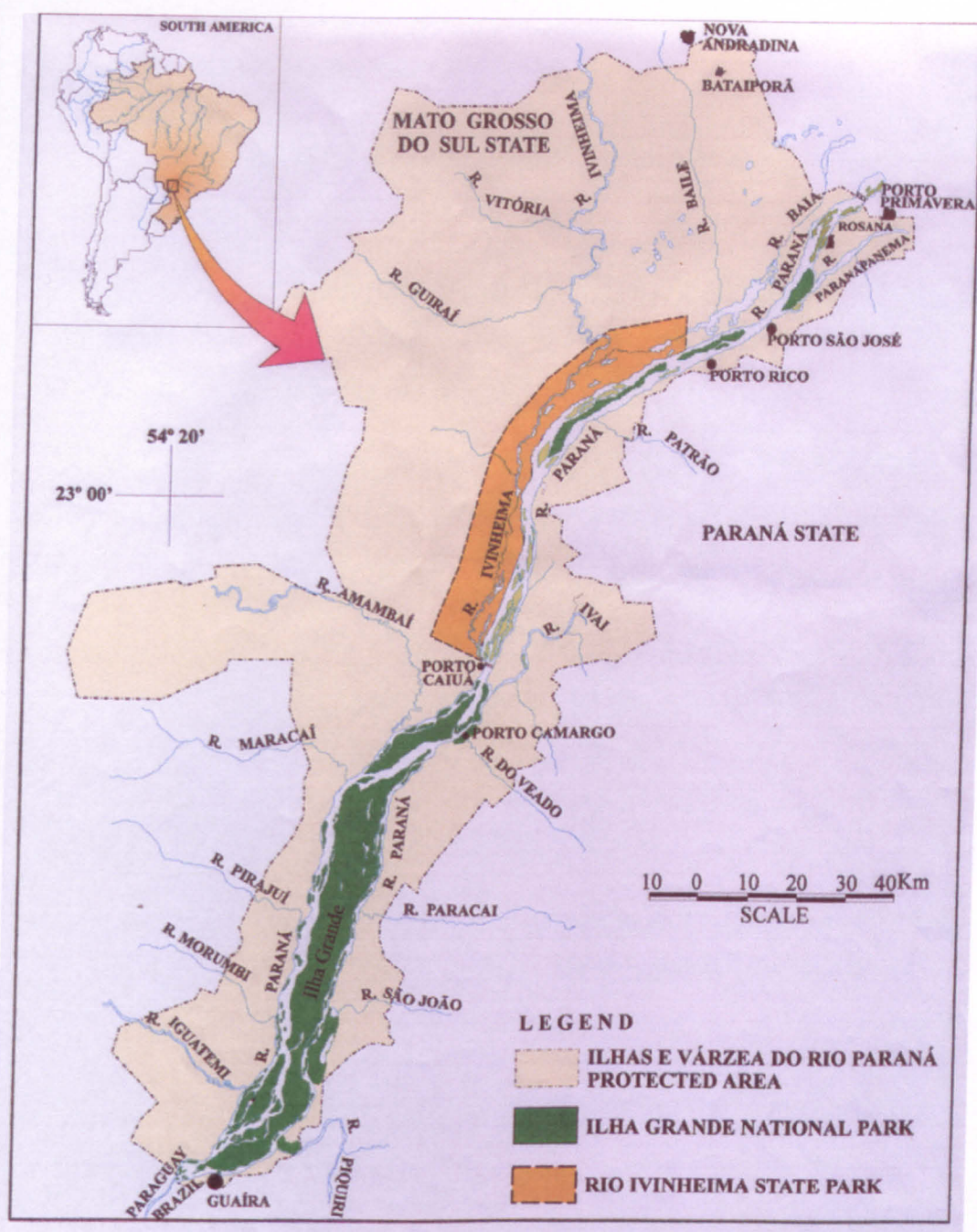


Figure 1.2 Conservation units in the floodplain of the Paraná River (Agostinho *et al.* 2000)

1.2 Project aims

The project aims to:

- 1 assess the current status of the floodplain vegetation;
- 2 model the principal environmental and human factors which regulate the vegetation;
- 3 quantify the threat to sustainability of floodplain plant communities which support small-scale agricultural grazing and provide habitat and breeding sites for commercially-important river fish populations;
- 4 provide data relevant to preparation of management strategies by the Brazilian environmental protection agencies responsible for protecting the floodplain habitats of the Paraná River and their plant and animal communities;
- 5 contribute to the knowledge-base needed by Brazilian agencies to develop and implement sustainable development programmes for small-scale agriculture and river fisheries in the Rio Paraná floodplain.

The specific questions that this thesis will address are:

- What types of dominant vegetation communities can be identified in three habitat zones within the floodplain (aquatic, bank or shore, adjacent floodplain areas)?
- What characteristics of the vegetation (in terms of collective vegetation variables and traits of dominant species), plus associated environmental characteristics, distinguish these communities?
- Which environmental and dominant species trait variables are effective predictors of collective vegetation characteristics such as community biomass and species richness?
- What effect does a single occurrence of severe biomass removal have on the structure of otherwise relatively undisturbed wet grassland vegetation?

- What effect does the removal of cattle grazing pressure have on the structure of formerly grazed island vegetation?
- How is the growth of three species of free-floating aquatic macrophytes affected by competitive interactions and nutrient availability?
- Do different species of aquatic macrophytes growing in the Paraná floodplain exhibit distinctive stable carbon isotope signatures?
- Can stable carbon isotope signatures be used to trace aquatic macrophyte carbon into a detrital food web?

1.3 Approaches

Each of the five results chapters of this thesis takes a different approach to meet the aims of the project. These approaches involve vegetation and environment surveys, field experiments, glasshouse experiments and a stable isotope study.

Chapter Two presents the results of the analysis of vegetation and environment surveys of a wide range of aquatic habitats conducted during the spring of three consecutive years (2000-2002). The current status of the aquatic vegetation of the floodplain is described by the identification of major vegetation types which are associated with contrasting ranges of environmental conditions (Aim 1).

The results of ordination analysis suggest environmental gradients which may be controlling the distribution and abundance of aquatic plant species across the floodplain waterbodies (Aim 2). The results of these analyses indicate which environmental factors can influence vegetation communities. If the floodplain is to be managed with the aim of maintaining the vegetation communities, it may be useful to monitor these factors in order to detect trends that could lead to disruption of the current vegetation status (Aims 4 & 5).

Regression analysis provides mathematical descriptions of relationships between vegetation characteristics and environmental factors (Aim 2). These allow prediction of the effects of potential future changes in environmental conditions on collective characteristics of the floodplain vegetation, such as biomass, species richness and physical structure. These vegetation properties are important because they influence the capacity of the vegetation to support other organisms. These results are therefore useful for

management of the floodplain, allowing potential problems to be anticipated and thus avoiding undesirable impacts on the vegetation (Aims 4 & 5).

Chapter Two also includes a section on morphological variation of two of the dominant species in the study area, *Eichhornia azurea* and *Eichhornia crassipes*. As these species are so common across the floodplain (particularly *E. azurea*), their distribution and abundance provide limited information about their responses to the environment. Variation in their morphological traits in relation to plant community type and environmental factors may indicate more clearly the factors regulating these two species which appear to play an important role in the aquatic plant communities of the floodplain. The results of this study were presented at the European Weed Research Society 11th International Symposium on Aquatic Weeds (Milne, Murphy & Thomaz 2002) and will be published shortly (Milne, Murphy & Thomaz 2004 in press).

In Chapter Three, approaches similar to those in Chapter Two are used to describe the vegetation of the banks or shores of the floodplain waterbodies and the adjacent floodplain areas. Species lists, collective vegetation data and outlines of the major vegetation groups provide information about the type of vegetation present in these locations (Aim 1). Comparisons of environmental factors between vegetation groups suggest the main influences on community composition (Aim 2). Regression analysis again indicates which factors are important in determining vegetation structure and provides a tool for prediction of the effects of future changes in environmental conditions in the floodplain (Aims 2, 4 & 5).

The effect of cattle grazing on the non-aquatic vegetation of the floodplain is investigated in Chapter Four. The use of the drier floodplain areas for livestock grazing is probably the main direct anthropogenic impact on the vegetation (personal observation), although large areas may also be destroyed by burning during the harvesting of wild Brazilian ginseng (*Pfaffia glomerata*) which is economically valuable. The historical need for land for pasture and crops has resulted in major deforestation in the whole of Paraná state.

Grazing impacts were studied using two approaches. In the first case, a simulated grazing treatment was applied to an area of apparently natural, undisturbed wetland grassland. In the second, the vegetation was already badly damaged by cattle grazing and the treatment applied was protection from grazing. The results of this chapter therefore provide information on the effect that grazing has on the vegetation of some areas of the floodplain (Aim 2). The capacity of the vegetation to tolerate and recover from grazing impacts is

also evaluated (Aim 3) and this information could be useful in management of the vegetation for grazing (Aim 5).

In Chapter Five, potential effects of the reduction in the frequency and duration of floods in the Paraná on floating aquatic plant communities are investigated in a series of competition experiments conducted in both low and high water nutrient level treatments. As flood events are important for nutrient cycling in tropical river floodplain systems, reduced flooding can be expected to result in a reduction in the nutrient status of floodplain waterbodies. As the disturbance caused by flooding is also reduced, it is suggested that competition becomes an increasingly important determinant of aquatic plant community structure. The results of the competition experiments describe how pairs of floating plants might interact under these conditions and what effect these interactions might have on their abundance and biomass (Aim 2). The experiments imitate predicted future conditions in the floodplain, and so the results provide useful information about how some species can be expected to respond if these conditions develop (Aims 3, 4 & 5).

Chapter Six aims to investigate one aspect of the biodiversity support role of aquatic macrophytes in the Paraná floodplain by attempting to evaluate their importance as a carbon source in aquatic food webs. This is often considered unimportant in comparison with their function as providers of habitats for other organisms. However, aquatic macrophyte production tends to be substantial in tropical river floodplains and so a number of studies have been carried out to try to establish the fate of the carbon fixed by aquatic macrophytes. This chapter considers a potential detrital pathway of carbon flow from aquatic macrophytes into the underlying sediment where it may be consumed by detritivorous invertebrates. Stable isotope analysis was employed with the aim of tracing carbon from aquatic plants with distinctive carbon isotope signatures into this detrital pathway. The carbon and nitrogen isotope signatures of some aquatic plants are presented and any relationships with the isotope signatures of the sediment are described. The potential contribution of aquatic macrophytes to the detrital carbon resource in the sediment at one site is suggested. The difficulties of employing stable isotope methods in the Paraná floodplain are discussed.

In the final chapter, the outcomes of each of the results chapters are brought together and discussed in the context of previous studies. The success of these outcomes in satisfying the original aims of the project is considered and future work that could help to improve understanding of the floodplain system and how to manage it is suggested. The overall conclusions of the study are highlighted.

1.4 The Paraná River: a regulated river-floodplain system

The Paraná River drains the 2.8 million square kilometre La Plata basin which spans southern Brazil, Paraguay, Uruguay and Argentina. It runs 4 495 kilometres from its headwaters at the confluence of the Paranaíba River and the Grande River in central Brazil to the Rio de la Plata estuary in Argentina where it reaches the Atlantic Ocean. Its major tributaries are the Paraguay River with its confluence at Corrientes in Argentina and the Iguaçu River with its confluence just downstream of the Itaipu dam in Brazil. The floodplain study area is upstream of these confluences in the Upper Paraná, a stretch of the river that was formerly delimited by the headwaters to the north east and the Sete Quedas waterfalls to the south west, now submerged by Itaipu Reservoir. In this study area, the unregulated Baía and Ivinheima Rivers enter the Paraná. The last remaining Brazilian stretch of semi-natural floodplain on the Paraná River now lies between Porto Primavera dam upstream (Figure 1.3) and the Itaipu Reservoir at Guaíba downstream. The area sampled during this project is a sub-section of this stretch, centred on the town of Porto Rico, 40 kilometres downstream of Porto Primavera.



Figure 1.3 Porto Primavera dam and reservoir.

1.4.1 Impacts of large-scale dams

The popularity of large-scale dam-building projects reached Brazil later than the rest of the world, where it peaked in 1968, and only became widespread in South America after 1970. However, by 1988, 96.2% of Brazil's total power production was being generated by hydroelectric schemes (Petts 1990). This exposed large, tropical, floodplain rivers of the continent to the detrimental impacts of river impoundment. In addition, these

developments tend to encourage changes in land use in the catchment such as urban growth, industrialisation, deforestation and agricultural development (Petts 1984). The overall effect of river regulation of floodplain environments is the loss of ecological integrity in the system (Petts 1996; Ward & Stanford 1995; Cairns 1995). The interaction of natural disturbance and connectivity of habitats is considered by Ward & Stanford (1995) to be the key to ecological integrity. Regular and predictable flooding resets sediment and vegetation successional processes while connectivity permits the movement of material and organisms between habitats and supplies propagules which stimulate primary succession at new colonisation sites. River impoundment inhibits the process of channel migration which both initiates and halts successional processes, leading to an environment characterized by a mosaic of habitats in different successional stages. High river flows are required to erode older stages and deposit sediment elsewhere where it serves as a seedbed for germination of pioneer species. Without this process, habitat heterogeneity is reduced and channel stabilisation permits establishment of terrestrial plant species (Ward & Stanford 1995). Natural river properties such as water velocity, turbidity, transparency and the degree of scour are strong determinants of aquatic plant distribution and so the alteration of these factors by river flow stabilisation or by the introduction of an erratic flood regime has a major effect on plant communities (Petts 1984). Colonisation by species adapted to a natural flooding regime may be prevented by artificial regimes if the degree of disturbance is too great or floods occur at an inappropriate time of year preventing the completion of life-cycles (Petts 1984). Regular flood pulses can be considered revitalising processes because the floodplain system is enriched with nutrients and because primary production and decomposition and life-cycle events, such as fish spawning, are stimulated. However, these events depend on connectivity in the aquatic ecosystems of the floodplain and exchanges between the floodplain and river channel which may be lost following dam construction.

A further impact of upstream dams may be the exacerbation of pollution problems because reduced flow erodes the “self-purification” capacity of a river (Petts 1990). However, there can also be an effect of reduced organic pollution downstream of a dam if phosphorus is retained in the reservoir sediments (Esteves 1983; Barbosa *et al.* 1999). Increased incidences of waterborne diseases have also been associated with the stagnant waterbodies created behind dams (Petts 1990). Damage to fish communities may occur because species are prevented from migrating by the barrier of the dam itself or due to loss of connectivity with the floodplain (Petts 1990; Agostinho, Thomaz & Nakatani 2002).

1.4.2 Hydrology of the Paraná

Prior to the construction of the many dams that now regulate water flow, the natural hydrologic regime of the Paraná was fairly regular throughout its length. Annual floods began between October and January and the low water period between April and July (Thomaz *et al.* 1992). The timing of these periods is thus variable, and in addition, the water is not consistently high or consistently low but fluctuates in pulses. However, the annual pattern of higher water spells in summer and lower water spells in winter is evident from water level data presented by Agostinho, Thomaz & Gomes (2004 in press) for the years between 1978 and 1997 (Figure 1.4). The occurrence of irregularities is highlighted by the unusual years of 1983 when water levels were particularly high and variable and 1986 when water levels were particularly low and less variable.

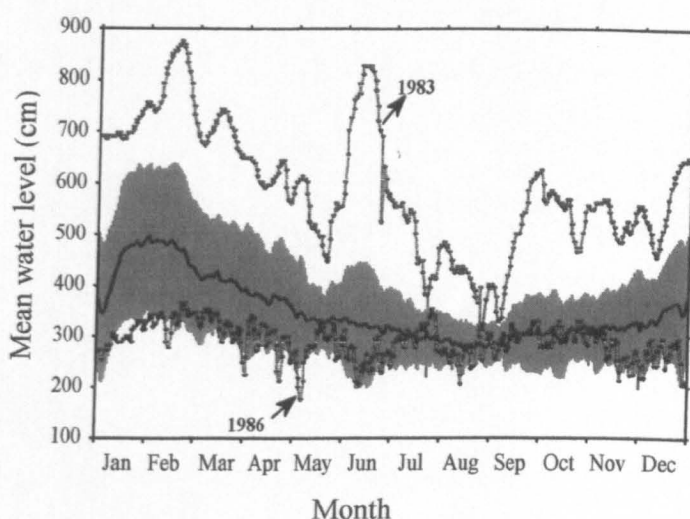


Figure 1.4 Mean water levels (\pm standard deviation) of the Paraná River at São Jose from 1978 to 1997 (shaded area) and water levels recorded in two unusual years, 1983 (exceptionally high and variable) and 1986 (exceptionally low and regular). Reproduced from Agostinho, Thomaz & Gomes 2004 in press.

Now the Paraná is the most regulated river in the world and so the natural water level and flooding regime has been altered (Agostinho *et al.* 2000). For example, before damming of the river began, the upper stretch consisted of a winding channel with riffles, rapids and waterfalls, most notably the Sete Quedas Falls, located downstream of the floodplain, which were comparable in size to the surviving Iguazu Falls. The loss of this natural barrier to migration has permitted at least 17 species of non-native fish to colonise the river upstream (Agostinho, Vazzoler & Thomaz 1995). Reservoirs such as the recently completed Porto Primavera scheme have directly destroyed upstream floodplain habitats

by inundating them. In addition, regulation of the natural flooding regime can have more insidious effects on floodplain habitats downstream.

The diagram of overall change in the hydrologic regime of the Paraná River since the series of dams was erected upstream of Porto Rico (Figure 1.4; Agostinho, Thomaz & Gomes 2004 in press) compares the previous unregulated discharge pattern with the more recent regulated pattern. The curves are similar in shape but the regulated discharge has a smaller amplitude representing a reduction in flood peaks during the high water season and an increase in water levels during the low water season. Water levels are therefore more consistent throughout the year and floodplain environments originally strongly influenced by flood pulses are homogenised. These changing water levels affect the relative sizes of aquatic, terrestrial and wetland habitats, the degree of connectivity between waterbodies, water depths and water velocities. These effects have been associated with changes in aquatic communities (Agostinho *et al.* 2000), limnological characteristics, nutrient cycling, biological production and successional processes (Thomaz, Roberto & Bini 1997; Ward & Stanford 1995).

1.4.3 Large, tropical river-floodplain systems

Floodplains have been defined in a variety of ways by geographers, hydrologists and ecologists. Marriot (1998) reviews definitions which depend on the topography and sediment type of the area adjacent to a river or on the limits reached by floodwaters over timescales of varying length. However, the ecological definition of floodplains given by Junk, Bayley & Sparks (1989) is more useful to describe the floodplain system of the Upper Paraná River: “areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physicochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic community structures”. The floodplain can be described as an “aquatic/terrestrial transitional zone” (Junk, Bayley & Sparks 1989) as it encompasses the lagoons, channels, tributaries, wetlands and terrestrial areas which are influenced by, and contract and expand in area according to, the annual rise and fall of river levels (Figure 1.5).

The floodplain therefore includes a range of habitats differentiated firstly by their hydrological status: lentic and lotic open waterbodies; transitional riparian and wetland zones; dry land islands. Bonetto (1975) describes vegetation zones in the floodplain of the Paraná River below its confluence with the Paraguay River. A gallery forest forms on

banks, the composition of which evolves as bank height increases. At lower elevations, this is replaced by *Panicum prionitis* and then *Solanum malacoxylom* which border lentic water. Shallow water at the edge of small pools may be colonised by *Ludwigia* sp. and *Polygonum* sp., or *Panicum elephantipes* or *Scirpus californicus*. In larger waterbodies, aquatic plants such as *Nymphaea amazonum* (rooted floating), *Myriophyllum aquaticum* (rooted submerged) and *Eichhornia crassipes* (free-floating) compete for light and space. Similarly, in the floodplain of the Amazon River, gallery forest dominates the dry land of banks and levees (Sioli 1975). At lower elevations, this is replaced by the wetland grasslands (várzea-campos) which tolerate dry conditions during low water levels as well as inundation during annual floods. In the lowest depressions are várzea lakes (Sioli 1975).



Figure 1.5 A large lagoon connected to the Baía River and bordered by várzea wetlands in the background. The dry levee in the foreground, which partially separates the lagoon from the river channel, supports terrestrial vegetation. The line of trees on the horizon also indicates a more terrestrial environment.

Annual floods in the Paraná and Amazon Rivers connect waterbodies with their floodplains and expose their vegetation communities to varying degrees of inundation, depending on topography and water level. As this is a regular, predictable event, plant and animal communities develop which can react to it by avoidance or adaptation (Junk 1986). In this way, habitats are further diversified which begins to explain the high number of species which tend to be associated with floodplain and wetland systems. The annual flood pulse has numerous effects on physical, chemical and biological characteristics of a floodplain. These include resetting successional processes, flushing out organic matter and phytoplankton, permitting exchange of dissolved chemicals and suspended sediments and providing linkages between waterbodies along which plant propagules and aquatic animals can migrate. The flood pulse is therefore considered to be the primary driving force

governing the ecological functioning of this type of system (Junk, Bayley & Sparks 1989; Thomaz, Roberto & Bini 1997; Heiler *et al.* 1995). The movement of material and organisms in large floodplain rivers is thus dominated by lateral processes in contrast with the nutrient spiralling described by the River Continuum Concept (Vannote *et al.* 1980) for headwater streams. In the River Continuum Concept, productivity in the lower stretches of a stream is considered to rely on inefficient upstream nutrient cycling losing organic material to the downstream current.

1.4.4 Influences of the flood pulse

Due to connection between waterbodies and inundation of drier areas during floods, the limnology and fertility of a floodplain are strongly influenced by the limnological characteristics of the river itself. Floodwaters tend to contribute dissolved inorganic compounds to floodplains but not organic material which is produced at greater rates in slow-flowing or transitional environments within the floodplain than in the main channel (Junk, Bayley & Sparks 1989). The greater the degree of connectivity between a floodplain waterbody and the main river channel, the more closely its hydrologic regime and limnological characteristics reflect those of the river. Conversely, more isolated lagoons on the interior of a floodplain experience water level changes with a time lag relative to changes in the river channel and the seasonal effect of flooding on limnology and aquatic communities is buffered (Thomaz, Roberto & Bini 1997). Heiler *et al.* (1995) compare the limnological conditions at low water and high water in waterbodies of varying connectivity in the floodplain of the River Danube. Flooding causes levels of nitrate and inorganic particles to increase in floodplain waterbodies but these quickly subside in poorly connected channels when water levels drop and internal floodplain processes became more important for nutrient and particle levels.

Thomaz, Roberto & Bini (1997) review several years of studies by researchers at UEM on the limnology of the Paraná River floodplain and its variation in relation to the seasonal water level regime. Relative to the waterbodies of the floodplain, the Paraná River has low values of total Kjeldahl nitrogen, total phosphorus and inorganic phosphorus and supports low densities of phytoplankton, as indicated by low chlorophyll-a concentrations. This means that the entrance of water from the Paraná River into the floodplain causes lagoons and channels to be diluted in these factors while the river water becomes enriched. However, phytoplankton communities do not develop in the channel because water turbulence and velocity are high. At the same time, the relatively low conductivity and

alkalinity of the floodplain waterbodies are increased by the contribution of inorganic salts from the river channel and by the decomposition of inundated plant material.

Water transparency of floodplain environments is greater during high water because suspended sediment in the water column is deposited. At low water, phytoplankton communities develop and sediment is resuspended by wind action, leading to low transparency. Dissolved oxygen is raised by the phytoplankton populations but is depleted during floods when decomposition of organic material increases.

During the low water period, floodplain habitats diversify according to local influences on their water chemistry and physical properties. However, annual flooding has a homogenising effect by connecting waterbodies and permitting exchange of dissolved compounds and suspended particles and organisms. Inundation causes decomposition of floodplain vegetation, facilitating nutrient cycling, and replenishes temporary lagoons which shrink in size or dry up during the dry season. Flooding therefore has a widespread and intense effect on the floodplain environments and so is largely responsible for the distribution and abundance of the plant and animal communities adapted to the resulting patchwork of habitats.

1.4.5 Biological diversity in the Paraná floodplain

The high diversity of species found in floodplain environments is consistent with a number of concepts concerning biodiversity. The floodplains of large rivers, such as the Paraná, have subtle variations in topography which result in aquatic and terrestrial habitats, depending on elevation, and ecotones between these. Therefore, species associated with both of these extremes and the continuum of hydrological conditions between them, as well as gradients of other environmental factors, occur in the floodplain. In addition, the entire floodplain has been described as an ecotone between two expansive vegetation types; the cerrado savanna of Mato Grosso do Sul state and the former semi-deciduous seasonal forest of Paraná state (Campos 1999a). The high productivity of the floodplain in conjunction with the annual flood, which results in intermediate disturbance to the system, could be predicted to lead to high herbaceous species richness according to Grime (1973). The variable degree of connectivity between floodplain aquatic environments is also associated with high biodiversity (Ward, Tockner & Schiemer 1999). The importance of regular flooding for plant diversity is illustrated by studies of the Rhône River in France which show greatest species richness and the highest occurrence of rare species in the most frequently flooded channels of the riverine wetlands (Bornette, Amoros & Lamouroux

1998). The authors associate this with the disturbance caused by floods that open up germination sites and supply plant propagules to colonise them from upstream.

Gopal & Junk (2000) draw attention to the importance of freshwaters and wetlands as hosts to a large proportion of world-wide biodiversity and point out the relatively small amount of attention paid to their study and preservation. The number of animal species associated with the floodplain environment exceeds those that are permanent residents. This is because some species migrate periodically from aquatic or terrestrial environments or from other wetland areas while others do not depend directly on the wetland status of the environment but are associated with vegetation or with other organisms that do (Gopal & Junk 2000). The lateral movement of biota from a river channel or terrestrial environment into a floodplain may drive speciation through subsequent adaptation to some range of the continuum of habitats that occurs there (Junk 2000). Tables 1.2 and 1.3 show the current figures for plant and animal species richness in aquatic, wetland and terrestrial environments obtained from surveys that have been underway since 1986 in the 230km undammed stretch of floodplain between Porto Primavera dam and the Itaipu reservoir (Agostinho, Thomaz & Gomes 2004 in press; Agostinho *et al.* 2000). During surveys of herbaceous vegetation conducted over several years on a 100km stretch of the Amazon River near Manaus, 330 terrestrial plant species, 34 aquatic plant species and 24 plant species of intermediate status were recorded (Junk & Piedade 1993b). 350 tree species have also been recorded in the seasonally inundated forest (Junk & Piedade 1993b). It is interesting to consider the Paraná figures in the context of the Amazon figures but, clearly, direct comparisons cannot be made due to the difference in sampling area and to likely differences in sampling technique and intensity.

Table 1.2 Number of species of aquatic organisms recorded in the Upper Paraná River and floodplain.

Aquatic organisms	Number of species
Phytoplankton	543
Periphyton	503
Macrophytes	60
Zooplankton	385
Zoobenthos	188
Fish	176

Table 1.3 Number of species of wetland/terrestrial organisms recorded in the Upper Paraná River and floodplain.

Wetland/terrestrial organisms	Number of species
Amphibians	22
Reptiles	37
Birds	351 (83 of original species locally extinct, 96 local colonisations)
Mammals	60
Flora	745

1.4.6 Human settlement and exploitation of north west Paraná state and the river floodplain

European settlement of the areas on either side of the Paraná River, where it now forms the boundary between the states of Paraná and Mato Grosso do Sul, started with the arrival of the Spanish in the sixteenth century. However, prior to this time, the land was already occupied by the indigenous Guarani tribes who modified the landscape by growing crops and clearing forest. The arrival of the Spanish and Portuguese led to violent confrontations with the indigenous people who were killed or enslaved by the Europeans or fell victim to the diseases they brought (Rosa 1997). At these early times, most economic activity was centred in the south of Paraná state and was based on gold in the seventeenth century and then erva-maté (South American tea) and timber in the nineteenth century.

The sequence of events which led to the current situation of settlement and exploitation of the north west of Paraná began in 1939 when a government-controlled colonisation programme was initiated. Immigrants from north east Brazil and São Paulo rented land and cleared it of forest in order to establish coffee plantations supplemented by subsistence farming of a few crops and animals (Agostinho & Zalewski 1996). Campos (1999a) collates data from three sources which illustrate the decline of forest cover in the area due to the arrival of settlers and changing land use in the hundred years between 1890 and 1990. Currently, 7.59% of Paraná state is forested compared to the original cover of 83.41% in 1890. In the mid 1960s, coffee was over-produced in Brazil and as a result, many plantations were turned over to pasture and cattle-raising became popular. This left many plantation workers unemployed and encouraged the colonisation of the islands of the Upper Paraná River which provided a refuge for them. Aerial photographs show that Porto Rico Island was almost completely covered by forest in 1952 but deforestation progressed

at a rapid rate after this time (Campos 1999a). The population remaining on the floodplain islands in 1982 and 1983 was finally expelled by the exceptionally high flood of that summer and cattle were subsequently put on the islands by large-scale landowners (Agostinho & Zalewski 1996).

Nowadays, few people inhabit the islands of the floodplain. Cattle are no longer permitted on the islands, which are now included in an Area of Environmental Protection, but some still remain illegally. A series of large, cattle-raising fazendas is situated along the Baía River and herds of cattle can be seen in some intensively grazed areas of the floodplain. As well as cattle raising, the floodplain supports professional fishermen, a sand-extraction industry and small-scale extraction of *Pfaffia glomerata* (Brazilian ginseng). Figures for the proportion of the population working in different types of industries are presented by Tomanik, Godoy & Ehlert (1997). Farming and ginseng extraction supports 10.6% of the population of Porto Rico while 7.4% have jobs associated with the river, including fishing and sand extraction. Five per cent of the population are professional fishermen although they are now prohibited from fishing during the spawning season, an action taken to preserve dwindling fish stocks. Illustrating a combination of socio-economic change and the inability of the floodplain to support the current population, 57% of the residents of Porto Rico have “urban” occupations which are not associated with the river and surrounding landscape at all (Tomanik, Godoy & Ehlert 1997).

1.5 Impacts of cattle grazing on island and floodplain vegetation

In many at least seasonally dry areas of the floodplain visited during fieldwork, there was strong evidence that the principal use made of these areas was as cattle pastures. Despite the prohibition of cattle on the islands of the main channel of the Paraná River, the occasional animal was still observed on Porto Rico Island and Mutum Island and the state of the vegetation at these locations suggested that the impact of grazing was still significant (Figure 1.6). Sward heights were frequently less than five centimetres with prostrate grasses forming a carpet broken up by occasional tussocks of taller grasses or shrubs. At one site, Entrada do Baía (EDB), the area of floodplain on the left bank of the river channel was an expanse of sparse, low vegetation on which a large herd of cattle were grazing (Figure 1.7). An alternative use of the land on the river banks and islands is banana and cassava cultivation, but only small-scale plantations were observed.



Figure 1.6 Bare ground and sparse vegetation on the dry levee between Lagoa do Osmar and the Paraná River on Mutum Island.

The importance of a minimal plant cover of some sort of vegetation, regardless of species, to the functioning of riparian rangelands is reviewed by Clary & Leininger (2000). Riparian vegetation is favoured by cattle, particularly during the dry season when it is more abundant than vegetation in other areas. Cattle impacts on herbaceous vegetation include the trampling action of their hooves and phytomass removal as they consume the plants. Trampling causes soil compaction and breaks up streambanks. In addition, grazing can cause alteration of the composition of plant communities. For example, the grazing of species which stabilise banksides but cannot withstand herbivore damage may lead to their replacement with others more resistant to herbivore damage but less able to stabilise banks. Banks then become even more vulnerable to erosion (Clary & Leininger 2000). Physical aspects of banks, such as large substrate particles, can make them less sensitive to these effects but the vegetation itself is still altered as the constraints on its survival vary in relative importance from stress to disturbance.



Figure 1.7 An area of recently burnt grassland in the floodplain of the Baía River where cattle were seen grazing (site code EDBc).

A study of wetland vegetation in European floodplains has shown that wetland plants are more likely to be adapted to survival pressures involving stress and competition than disturbance, the three determinants of plant survival described by Grime (Grime 1977; Hills *et al.* 1994). Stress occurs through the limitation of factors necessary for photosynthesis and is imposed, for example, through flood and drought events. Competition occurs due to the survival advantage of being efficient in obtaining these factors in habitats where other pressures are less significant, for example, in highly productive wet grasslands. In the absence of farming impacts, disturbance pressures probably consist mainly of the annual flood events, which are relatively predictable.

The adaptation of plant communities to environmental sources of stress and competition has resulted from historical conditions in the floodplain and does not provide resistance to the anthropogenically-imposed disturbance impact of grazing that has occurred over the past 50 years. Other herbivorous animals, including deer and capybara, occur naturally in the floodplain but their disturbance impacts can be considered minimal compared to the degradation of vegetation observed in cattle enclosures. In heavily grazed areas, the constraints on survival of a natural floodplain species are supplemented by disturbance and so its survival strategy ceases to match the local conditions. It can be predicted that such species will be replaced by others which are more disturbance-tolerant. The result is that overall plant community functional type can be expected to tend towards greater disturbance-tolerance while stress-tolerance components may be reduced due to the stabilisation of the river flow regime resulting from upstream regulation.

The direct effects of consumption of plant biomass are experienced principally by Poaceae and Cyperaceae as these are the families selected both by cattle and by capybara, one of the native herbivores of the region (Quintana, Monge & Malvárez. 1998). In studies of the two herbivores grazing in the Lower Delta of the Rio Paraná in Argentina, their diets have been found to consist of a small number of species such as *Cynodon dactylon*, *Panicum grumosum*, *Zizaniopsis bonariensis* and *Eleocharis* spp. (Quintana, Monge & Malvárez. 1998). The introduced cattle thus consume the same types of species as the native capybara but at a much higher intensity due to high stocking rates and restriction of their feeding to particular areas through fencing. The much larger size of the animals and their hard hooves result in greater damage to soil and vegetation compared with capybara. The long term territoriality of capybara, which tend to remain within a home range, favours self-controlled regulation of their food consumption as a group could not survive in a limited area if it exhausted the food sources all at once (Barreto & Herrera 1998). Given the choice, cattle prefer not to graze extremely short vegetation as the forage intake level is greatly improved if they move on to taller vegetation. The low sward height observed on Porto Rico Island therefore implies that the cattle may need to browse trees in an effort to supplement their diet (Clary & Leininger 2000).

Inausti, Chaneton & Soriano (1999) suggest that flooding events in Argentinian grasslands may reverse the effects of grazing. They consider these two controls on plant community structure to be opposing in the sense that flooding is a stress factor and grazing is a disturbance factor and plants that tend to be tolerant of flooding stress tend to be intolerant of grazing disturbance. This suggests that the reduced flooding of the Paraná River into its floodplain could exacerbate the damaging effects of grazing. Inausti, Chaneton & Soriano (1999) found that formerly grazed mesocosms which were flooded for a period had greater total and particularly graminoid biomass than grazed mesocosms which were not flooded. In addition, the biomass of seven out of ten graminoid species increased during the flooding. The greater recovery of graminoids compared to other herbaceous species is significant considering these are preferred by the herbivores. However, the combined effects of flooding and grazing on the growth and survival of a particular species depend on the adaptations which that species possesses to each of these pressures. Species which do not display adaptations to flooding will be killed during long periods of submergence while those with poor resistance to grazing may be killed through loss of photosynthetic tissue and growing points. For example, *Eleocharis acuta* can withstand flooding if it is undamaged or will survive simulated grazing due to the location of its meristems below ground, although with reduced growth in both cases, but a combination of both pressures results in high mortality rates in experimental conditions (Blanch & Brock 1994).

The loss of flood events in the floodplain can also be expected to have long-term effects on its fertility and consequently on the vegetation. Nitrate and phosphate levels of waterbodies in the floodplain naturally vary widely due to the influences of both the river floodwaters and local environmental conditions (Thomaz, Roberto & Bini 1997). The inputs of nutrients into areas of higher elevation only submerged during the wet season is also affected by the floods which influence nutrient cycling rates or may deposit sediments on the floodplain floor. The absence of floods on the Upper Paraná in recent years may still be within the range of what could be considered natural conditions, as exceptionally high or low water levels for the duration of a whole season are not unknown (Thomaz, Roberto & Bini 1997). However, even if floods resume, it can be expected that the flooded area will be reduced due to continued regulation of water flows limiting water levels in the wet season. Changes in fertility in some more elevated parts of the floodplain can therefore be anticipated. The combined effects of this factor and others such as grazing, which is likely to be encouraged by the exposure of new dry areas, are relevant to the potential conversion of the floodplain vegetation from a natural to an artificial state.

Two experiments were designed to investigate aspects of grazing impacts and changing soil nutrient status on floodplain vegetation structure. These involved two approaches for the comparison of grazed vegetation with ungrazed vegetation and therefore assessment of grazing impacts on vegetation. The first approach involved simulating grazing by cutting down vegetation. The effect of this disturbance on vegetation recovery after a fixed period was assessed by comparison with uncut vegetation. The second approach involved protecting small areas of vegetation from grazing effects using exclosures and comparing the protected vegetation with adjacent unprotected vegetation. The interaction of this factor with nutrient supply was also investigated through the application of fertiliser.

1.6 Potential consequences of changing flow regime in the Paraná for competition between aquatic plants

1.6.1 Likely impacts of river regulation on the nutrient status of floodplain waterbodies

In the aquatic vegetation communities of the floodplain, grazing by livestock or other large herbivores does not seem to have a significant impact (personal observation). Aquatic macrophytes may support high densities of invertebrates, some of which feed upon plant material. For example, Poi de Neiff & Casco (2003) showed that two species of

Neochetina and an unknown species of *Thrypticus* caused extensive damage to the petioles of *Eichhornia crassipes* in the floodplain of the Paraná River in Argentina. However, grazing by these three species did not result in reduced plant cover or in significant losses of leaves. Pressures shaping aquatic macrophyte species composition, vegetation structure and biomass are more likely to be concerned with the flow regime and water chemistry of the river. Current knowledge of the influence of the natural annual flood on the Paraná River permits hypotheses to be formulated of the likely impacts of disruption of this process, principally in the form of reduction of its scale and longevity. Limnological studies carried out by the Nucleus of Researchers in Limnology, Ichthyology and Aquaculture (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, NUPELIA) at the State University of Maringá (Universidade Estadual de Maringá, UEM) (Thomaz, Roberto & Bini 1997) have tracked the changing fertility of the waters of the various waterbodies and channels of the Paraná floodplain in Mato Grosso do Sul state in response to the annual flood. These responses vary depending on the degree of connectivity between a waterbody and the main channel, with várzea lagoons and semi-lotic habitats being most strongly influenced (Thomaz, Roberto & Bini 1997). The timing of peaks in nitrogen and phosphorus levels in these waterbodies has been identified. At the end of the dry season, when the floodplain and island lagoons are at their lowest level, electrical conductivity, total Kjeldahl nitrogen and total phosphate contents of várzea pools reach a peak due to wind action or cattle trampling stirring up sediment, resulting in the release of phosphorus. A second peak in phosphorus occurs when the level of the Paraná is rising at the beginning of the wet season. Vegetation on the previously dry floodplain is inundated by flood water and decomposition results in further release of phosphorus, nitrogen and other plant nutrients (Thomaz, Roberto & Bini 1997). During the flood peak, inflow of the phosphorus-poor waters of the Paraná results in a decline in phosphorus levels in the floodplain due to dilution (Agostinho & Zalewski 1995; Thomaz *et al.* 1992). However, this influx also brings inorganic nitrate and other salts resulting in a peak in water inorganic nitrate content, alkalinity and electrical conductivity.

A reduction in the scale of flood events suggests a reduction in the scale of nutrient cycling processes which they stimulate. Retention of floodwaters in upstream reservoirs of the Paraná restricts the volume of water reaching the floodplain and consequently reduces the area, depth and duration of inundation. This is anticipated to result in reduced rates of vegetation decomposition. For example, the rate of loss of dry weight of *Eichhornia azurea* has been shown to decrease as the duration of its submergence decreases, with the slowest rates of decomposition recorded when no submergence occurs (Thomaz *et al.* 2003). Other effects of reduced flooding include reduced inputs of nitrate and other salts

to the floodplain and failure of replenishment of seasonal lagoons with fresh water. In addition, phosphorus is lost from the Paraná River when it precipitates out of the water and accumulates in the sediments of upstream reservoirs where it remains trapped (Thomaz, Roberto & Bini 1997; Esteves 1983; Barbosa *et al.* 1999). The complex processes of nutrient release from decomposing vegetation and sediments and nutrient inputs and dilutions by river water make it difficult to predict patterns of water nutrient changes likely to result from reduced flood events. However, the net effect implied from the processes described is likely to be a general decline in nutrient cycling and consequently lower nutrient status of floodplain waterbodies.

1.6.2 The stress/disturbance/competition balance

As described previously, the fundamental importance of the annual flood pulse to the functioning of floodplain ecosystems (Junk, Bayley & Sparks 1989) means that alterations caused by flow regulation through damming have widespread and diverse effects on all kinds of physical and biological processes. Changes in the fertility of the floodplain and its waterbodies are at the start of a chain of effects which are first passed on to primary producers and then on to the organisms which they support. As consumers of the phosphorus and nitrogen in the lagoons and channels of the floodplain, aquatic macrophytes are directly affected by changes in their concentrations. If the growth of a particular species is determined by the intensity of pressures summarised by Grime (1977) as stress, disturbance and competition, the alteration in the relative importance of these pressures by an increase in the productivity of a habitat will affect vegetation biomass and community composition. Plant biomass accumulation is regulated by the availability of nutrients and other factors necessary for growth. The capacity of a particular species to obtain these factors in a low nutrient environment (*i.e.*, its stress-tolerance ability) will determine whether or not it can grow there successfully. However, if nutrients are in plentiful supply, the capacity of a particular species to compete with others for space and growth factors (*i.e.*, its competitive ability) will be the greater determinant of community composition (Grime 1977). The nutrient status of floodplain habitats thus has a controlling influence on plant community composition, distribution and biomass. This influences the quantity and diversity of habitats which aquatic vegetation can provide for other organisms, such as zooplankton (Lansac-Tôha, Velho & Bonecker 2003) and invertebrates (Takeda *et al.* 2003). Patterns in these organisms in turn determine the quantity and type of animals, such as fish, which can be supported in the next level of the food chain. As well as a food source, macrophytes also provide shelter and breeding sites for fish, and

nurseries for fry (Agostinho & Zalewski 1995, Agostinho, Gomes & Júlio Júnior 2003). For example, Agostinho *et al.* (2002) found that fish abundance and species richness were maximised at the margins of stands of *Eichhornia azurea* when compared with the middle of plant stands and with open water in the Baía River. In the Brazilian floodplain of the Paraná River, disturbance is obviously a major pressure on plant survival due to the large-scale floods which, under natural conditions, annually wash away or drown aquatic vegetation. However, during the growing season after the floods subside, habitats are much more stable. The fertilisation of the water and floodplain by the flood pulse results in very productive habitats favourable for plant growth. Under these conditions of low disturbance and low stress, competitive interactions between plants become most important for determining plant success and survival (Grime 1977). Populations of free-floating plants such as *Pistia stratiotes*, *Salvinia* species, *Eichhornia crassipes* and *Limnobium laevigatum* can recover very quickly by vegetative reproduction from remaining plant fragments. The relative success of each of these functionally similar species is therefore likely to depend on differences in their abilities to compete for space, nutrients and light in a reasonably favourable habitat. However, if plants are also subjected to a source of stress, such as the potential reduction in nutrients in the floodplain, the outcome of competitive interactions may vary from the outcome in less stressed conditions, such as those which existed prior to the recent major disruption of the flood regime. It is therefore interesting to investigate competitive interactions between species under both low and high nutrient availabilities.

The effects of the changed flooding regime on nutrient status are likely to vary across the floodplain depending on local conditions such as proximity to flowing channels which may overflow, amounts of vegetation storing nutrients and inputs of nutrients from cattle fields or fertile tributaries. As floating plants depend entirely on water nutrients for growth and survival, they are likely to respond to changes in availability of nitrogen and phosphorus in the water. In order to investigate the effects of varying nutrient availability and competition intensity on pairs of floating aquatic plant species, a series of three glasshouse experiments was designed.

1.6.3 Competition theory

Competition is defined by Grime (1973) as “the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space”. This describes the driving force behind competition, which is the common need for similar resources shared by plants. Keddy’s (1989) definition of competition, “the

negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability", is concerned with the impact that this tendency has upon the plants. The view of competition taken in Chapter Five is consistent with both of these definitions. Here it is considered as the suppression of growth of individuals or populations resulting from their interaction with other individuals or populations.

A competitive plant may suppress the growth of neighbouring plants by highly efficient resource acquisition, leaving a depleted resource pool, or by directly inhibiting resource acquisition by its neighbours (Keddy 1989). Competition may be symmetric if all neighbours have well-matched competitive abilities. However, if dominant and subordinate individuals or populations emerge due to differences in competitive ability, competition is asymmetric and some neighbours are more successful than others.

Although competitive interactions result from resource limitation, competition may be considered to be most significant in structuring plant communities in resource-rich, productive habitats (Grime 1977). In habitats subject to stress or disturbance pressures, the most successful species are those with the adaptations that allow them to tolerate these conditions. Species tend to be present or absent depending on their capacity to survive chronically low resource levels or regenerate following disturbance. Plants lacking these adaptations are restricted to habitats where growing conditions are very favourable and vegetation can reach high levels of biomass. In this situation, the plants likely to be successful are those with highly efficient resource acquisition mechanisms or the ability to suppress neighbouring plants so that they can dominate in competitive interactions. The successful species benefit from a positive feedback effect as their relatively high rates of resource uptake lead to increased growth, which further increases their ability to exploit resources (Keddy 1989). Variation in the relative importance of traits for stress tolerance, disturbance tolerance and competition is illustrated in a study by Wilson & Keddy (1986), which demonstrated an increasing competitive ability of shoreline plants growing along a natural exposure gradient of decreasing stress (soil nutrient shortage) and disturbance (wave action). In another experiment, the impact of neighbouring aquatic plant communities on the growth of species transplanted in cleared or vegetated plots along a gradient of water depth, soil organic matter and standing crop was considered (Wilson & Keddy 1986). Survival of the transplants was lower in the presence of neighbours than in cleared plots at the productive end of this gradient where standing crop was high, water was shallow and soils were organic. At the less productive end of the gradient, there was little difference in transplant survival between cleared and vegetated plots. This suggested

that the competitive ability of the neighbouring community was greatest in the most productive habitats, agreeing with the earlier study. However, the effect of neighbouring plants on the biomass of the transplants did not vary along the gradient and it was concluded that competition was not playing an important role in structuring the macrophyte community.

In field conditions, competition may occur between the species or populations comprising a community. This may be studied by manipulating the community by adding or removing species. Removal allows any inhibitory effect of the removed species on the other members of the community to be studied (*e.g.*, Chambers & Prepas 1990). This provides information about competitive interactions occurring in the natural assemblage. Addition of a species creates an artificial scenario allowing the impact of the introduced species on the original community to be studied, or vice-versa. This may be useful for studying the potential impact of a new species should it invade the existing community. In contrast, Wilson & Keddy (1986) used transplants to evaluate the competitive ability of plots of existing vegetation.

Controlled experiments where the study species are selected and transplanted into experimental units create highly artificial conditions but allow the relative competitive ability of pairs of species to be studied. Through study of a series of these pairwise interactions, competitive rankings between sets of species can be elucidated (*e.g.*, Keddy, Twolan-Strutt & Wisheu 1994). Pairwise studies in pots or tanks have also been conducted with submerged aquatic macrophytes (*e.g.*, Abernethy, Sabbatini & Murphy 1996; Spencer & Ksander 2000) and free-floating species (*e.g.*, Agami & Reddy 1990; 1991; Reddy & DeBusk 1984).

1.6.4 Design of competition experiments

Agami and Reddy (1990; 1991) apply the replacement series design for investigation of competitive interactions between pairs of species (de Wit 1960) to floating aquatic plants. This design is based upon keeping overall plant density equal in each competition treatment whether it consists of one species growing in monoculture or a mixed culture of both species. However, it is difficult to apply this principle in the case of *Salvinia auriculata*, a clonal plant which can be broken up by disturbance into many pieces, each of which is a viable independent plant. Although *Pistia stratiotes* and *Limnobium laevigatum* also reproduce vegetatively, each daughter plant is recognizable as a distinct individual rosette. This was overcome in the experimental design by trimming *S. auriculata* plants

for use in treatments so that they were of a comparable size to each other. The replacement design permits calculation of the competitive ability of each species in relation to the other as an “aggressivity score” (McGilchrist & Trenbath 1971) and the effect on yield of the species pair grown in mixed culture compared to pure culture as “relative yield total” (de Wit & van den Bergh 1965).

An additive design can potentially overcome the problem of trying to define plant density. In this case, the amount (phytomass or plant density) of the species under study is kept constant in all treatments while a second species is added to impose competitive interactions. Competition can be applied at different levels, for example, none (only one species present), low intensity (a small number or mass of the competitor added) or high intensity (a large number or mass of the competitor added). However, useful information is obtained about only one of the species in an additive experiment and relative yield total and aggressivity cannot be calculated because only one species is grown in pure culture and there is no mixed treatment consisting of an equal density mix. The replacement design was therefore chosen for use in the series of experiments because it provides more information than an additive experiment of comparable size permitting conclusions to be drawn about the competitive ability of both species in each experiment.

1.6.5 Study species

Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine (Hydrocharitaceae) is a small, stoloniferous, rosette species which may be free-floating or bottom-rooted. It is native to temperate and tropical America (Cook 1990a). The leaves can take two forms depending upon the age of the plant or the degree of crowding by other plants (Sculthorpe 1967). In young plants or in uncrowded habitats, the leaves are very spongy and rounded and lie flat on the water surface. In older plants or in more crowded conditions, the petioles become upright and the leaf blades more oblong. The well-developed lacunate mesophyll of the leaf blade provides buoyancy (Sculthorpe 1967). The flowers are wind-pollinated and the seeds dispersed by water or by animals (Cook 1990a) although vegetative reproduction via stolons is also important.

Like *Limnobium*, *Pistia stratiotes* L. also has a rosette form and is stoloniferous. Its modern distribution is pantropical (Cook 1990a) but its native range is uncertain due to its rapid spread through the world before this was recorded (Cook 1990b). It is limited to warmer areas as it is not tolerant of frost and can be killed by freezing (Reddy & DeBusk 1984). The flowers are insect-pollinated and the seeds dispersed by water (Cook 1990a)

although reproduction from seed is much less important in population growth than the vegetative development of new plants on the stolons of parent plants (Spencer & Bowes 1990). Vegetative reproduction permits this species to grow very quickly and produce high levels of biomass. Reddy & DeBusk (1984) studied the growth characteristics of *Pistia* in nutrient-enriched water in Florida. The doubling time for dry weight at low plant density was only 3.9 days and annual biomass yield was calculated as 72 tonnes dry weight $\text{ha}^{-1} \text{yr}^{-1}$ (Reddy & DeBusk 1984). This capacity for rapid growth means that *Pistia* can become a problem weed. Aquatic weeds can have a number of negative effects including blocking navigation routes and irrigation or drainage channels, interfering with fishing, recreation and other uses of the water, trapping silt and increasing sedimentation, and increasing water loss through evapotranspiration (Pieterse 1990).

Salvinia auriculata Aubl. (Pteridophyta, Salviniaceae) is a free-floating fern with forked stems and no roots. Leaves are in whorls of three, one of which is submerged, non-photosynthetic and root-like. *S. auriculata* spreads by fragmenting but also produce spores from sporocarps on modified submerged leaves, although the viability of the spores is unknown (Cook 1990b). Most studies of the *Salvinia* genus have focused on one particular species, *S. molesta*, which causes major weed problems (Pieterse & Murphy 1990). Cook (1990b) reports that it is believed to be a horticultural hybrid of *S. biloba* and possibly *S. auriculata*. However, *S. molesta* is also an acceptable synonym for *S. auriculata* (W³TROPICOS database) and so it is not clear whether or not it is a separate species. Sale *et al.* (1985) studied the photosynthetic and growth properties of *S. molesta* to try to understand why it is such a troublesome weed. They found that it had relative growth rates for dry weight in uncrowded, summer conditions in Australia of $0.11 - 0.16 \text{ g g}^{-1} \text{ d}^{-1}$ but that this rapidly declined in crowded conditions. The extraordinary capacity of *S. molesta* for rapid colonisation across a water surface appeared to be because it avoided overcrowding for as long as possible by continually floating into new open areas of water where the relative growth rate could be kept near maximum (Sale *et al.* 1985). Even if *S. auriculata* is a different species from *S. molesta*, it spreads and reproduces in the same way and so probably also has the capacity to maintain a high relative growth rate for as long as there is open water available.

1.7 Macrophytes as a carbon source for aquatic food webs

1.7.1 Ecosystem support role of aquatic macrophytes

Aquatic macrophytes play a variety of roles in supporting aquatic biodiversity by providing architecturally diverse physical substrates for colonisation by epiphytes and invertebrates and oviposition sites and sheltered nurseries for fish (Sculthorpe 1967). They also create gradients of light, temperature, oxygen concentration and pH within the aquatic environment, influence water velocity and patterns of silt deposition and stabilise river banks (Westlake 1975). The diverse community of algae, bacteria and protozoa mixed with detrital particles found on submerged leaf surfaces (aufwuchs) provides a rich food resource for invertebrates and fish (Moss 1998). Aquatic macrophytes and their fruits and seeds may also provide food for invertebrates, fish, waterfowl and mammals (Sculthorpe 1967; Lodge 1991). For example, the aquatic snail *Lymnaea stagnalis* will consume a number of submerged macrophyte species at rates dependent upon the age of the plant tissue and the degree of plant investment in herbivore defences (Elger, Barrat-Segretain & Amoros 2002). Feeding trials and field observations have shown that *Nuphar variegata* and *Nymphaea odorata*, amongst other species, are consumed by a larval caddisfly, *Limnephilus infernalis*, as well as three partially aquatic and one primarily terrestrial invertebrate, each of which has its own plant preferences and degree of specialisation (Cronin, Wissing & Lodge 1998). Laboratory experiments and field observations in Cayuga Lake, New York, USA have shown the preference of the larval aquatic moth, *Acentria ephemerella*, for *Myriophyllum spicatum* over *Elodea canadensis*, which may have been involved in a shift in dominance from *Myriophyllum* to *Elodea* in the lake (Gross, Johnson & Hairston 2001). Fish stomach content analysis has shown that some fish species consume significant amounts of macrophyte tissue. For example, *Schizodon fasciatus* consumes C₄ grasses (Forsberg *et al.* 1993) and *Mylossoma duriventre* consumes macrophyte seeds (Benedito-Cecilio *et al.* 2000) in the Amazon. The Paraná species *Pterodoras granulosus* also consumes flowers, fruits and seeds of a number of plants, including emergent macrophytes (Souza-Stevaux, Negrelle & Citadini-Zanette 1994). Aquatic plant material may also contribute to the detrital food resource when plant parts become detached and are broken down by microorganisms. Many fish and invertebrate species rely on this complex of decomposing plant and animal remains, faeces, microorganisms and inorganic particles for food (Hynes 1970).

For the animals mentioned above, aquatic macrophytes clearly do provide an important source of food and enter some aquatic food webs. However, in comparison with the aufwuchs communities inhabiting the surfaces of submerged plants, the role of macrophytes as a food source is often considered to be minimal (Hutchinson 1975). Few stream invertebrates possess the feeding adaptations required to consume living plant tissue (Cummins & Klug 1979). Stable isotope analysis provides a tool for understanding the seeming paradox of high production of aquatic macrophytes in some systems yet minimal contributions of macrophyte carbon to aquatic food webs (Araujo-Lima *et al.* 1986).

1.7.2 Naturally occurring stable isotopes

The naturally occurring stable isotopes of carbon and nitrogen differ in their atomic mass due to additional neutron particles present in the nuclei of the heavier isotopes, in this study ^{13}C and ^{15}N . These heavy isotopes occur at low concentrations in relation to ^{12}C (1.10% of global carbon is ^{13}C) and ^{14}N (0.37% of global N is ^{15}N) (Criss 1999). Different sources of carbon and nitrogen vary in the ratio of the heavy to light isotope which they contain due to processes which discriminate between the isotopes (Criss 1999). The stable isotope ratio for carbon is expressed as $\delta^{13}\text{C}$. This describes enrichment in the heavy isotope in parts per thousand relative to an international standard limestone, Pee Dee Belemnite:

$$\delta^{13}\text{C} (\text{‰}) = [((^{13}\text{C}/^{12}\text{C} \text{ sample}) / (^{13}\text{C}/^{12}\text{C} \text{ standard})) - 1] \times 1000 \text{ (Criss 1999)}$$

$\delta^{15}\text{N}$ is calculated similarly, but is quoted relative to the standard atmospheric nitrogen.

Carbon isotopes provide a tool for analysing carbon transfer within biological systems because assimilation during successive trophic levels has little impact on $\delta^{13}\text{C}$ (Peterson & Fry 1987). A literature review of estimates from 22 studies has suggested a mean fractionation during assimilation of -2.1 to $+2.8\text{‰}$ with a mean of $0.47 \pm 1.23\text{‰}$ (1 SD) (Vander Zanden 2001). Therefore, $\delta^{13}\text{C}$ of a consumer is very similar to $\delta^{13}\text{C}$ of its food source. In the case of primary production, isotopic fractionation occurs largely because the carboxylation enzyme involved in photosynthesis, ribulose biphosphate carboxylase/oxygenase (rubisco), reacts preferentially with carbon dioxide molecules possessing the lighter carbon isotope (Wong, Benedict & Kohel 1979). $\delta^{13}\text{C}$ of atmospheric CO_2 is -7‰ and the fractionation effect attributable to rubisco has been

measured as approximately -27‰ (Wong, Benedict & Kohel 1979). Measurement of $\delta^{13}\text{C}$ of a range of species of plants in which the C_3 photosynthetic pathway operates was found to vary from -22 to -33‰ in one study (Bender 1971) and from -24 to -34‰ in another (Smith & Epstein 1971). Variation in plant $\delta^{13}\text{C}$ may be due to other factors which influence the degree of isotopic fractionation, such as CO_2 concentration in the leaf and the abundance of CO_2 derived from respiration or industrial processes (O'Leary 1981). In species in which the alternative C_4 acid pathway operates, the initial fixation of atmospheric CO_2 is by phosphoenolpyruvate carboxylase in the mesophyll cells into C_4 acids (Salisbury & Ross 1992). These acids are then transported to the bundle sheath cells where CO_2 is released and refixed by rubisco. Rubisco can bind either CO_2 or O_2 resulting in photosynthetic carbon reduction or photorespiratory carbon oxidation respectively (Salisbury & Ross 1992). The C_4 mechanism improves photosynthetic efficiency by concentrating CO_2 in the rubisco-containing cells where O_2 is absent, maximising carbon reduction and minimising oxidation (Salisbury & Ross 1992). During this process, carbon isotopes are discriminated to a much lesser extent than in C_3 photosynthesis and plant $\delta^{13}\text{C}$ values of -10 to -20‰ (Bender 1971) or -6 to -19‰ (Smith & Epstein 1971) may be measured. The contrasting $\delta^{13}\text{C}$ of the C_3 and C_4 plant groups makes carbon isotope analysis particularly suitable for investigating fish carbon sources in rivers where the majority of aquatic macrophytes are of the C_4 type and can therefore be distinguished from C_3 riparian vegetation and phytoplankton, for example, in the Amazon and Orinoco rivers (Lewis *et al.* 2001; Forsberg *et al.* 1993).

Submerged aquatic macrophyte photosynthesis (SAM) does not correspond directly with the terrestrial mechanisms and is not so well understood. In the aquatic environment, the supply of CO_2 can limit the rate of photosynthesis due to the diffusional resistance of unstirred layers of water surrounding plant organs (Smith & Walker 1980) or because of high levels of consumption by dense stands of macrophytes. Submerged plants therefore have developed adaptations to enhance the uptake of inorganic carbon and to increase the efficiency of rubisco (Bowes 1987). Some species employ a C_4 acid pathway similar to terrestrial C_4 plants in order to concentrate CO_2 and reduce the oxygenase activity of rubisco (*e.g.*, *Hydrilla verticillata*), while others are able to use HCO_3^- ions as a source of carbon, for example *Myriophyllum brasiliense* (synonym *M. aquaticum*) (Bowes 1987). In addition, hydrosol CO_2 may be accessed by well-developed root systems (*e.g.*, *Littorella uniflora*) or atmospheric CO_2 by aerial leaves (*e.g.*, *Myriophyllum brasiliense* (synonym *M. aquaticum*)) (Bowes 1987).

Carbon isotope fractionation in submerged aquatic plants therefore depends on which of these adaptations occurs in a particular species. Different sources of HCO_3^- and CO_2 will also affect plant $\delta^{13}\text{C}$, for example HCO_3^- derived from limestone is more enriched than atmospheric CO_2 , while CO_2 produced during plant decomposition is particularly depleted (Osmond *et al.* 1981). Osmond *et al.* (1981) show the variation observed in plant $\delta^{13}\text{C}$ between habitats varying in carbon source and water velocity. Water velocity can cause variation in submerged plant $\delta^{13}\text{C}$ because of its effect on the rate of diffusion of carbon to leaf surfaces. In still water, slow diffusion may result in a low supply of carbon to rubisco, which then reacts with all available isotopes without discrimination (Smith & Walker 1980; Keeley & Sandquist 1992) leading to $\delta^{13}\text{C}$ close to the value of the carbon source.

Because carbon source, diffusional resistance, the activity of acid pathways, the rate of use of bicarbonate ions and the development of aerial leaves are all influenced by environmental conditions, submerged plant $\delta^{13}\text{C}$ can be expected to vary spatially and temporally.

Nitrogen isotopes cannot be used to trace the fate of plant material because nitrogen sources are more diverse and plant $\delta^{15}\text{N}$ much more variable than $\delta^{13}\text{C}$. Soil $\delta^{15}\text{N}$ may vary greatly according to the local pattern of nitrogen inputs, such as decaying animals, symbiotic N_2 fixing plants and fertiliser applications, and the process of uptake and assimilation by plants does not involve a simple, predictable fractionation (Handley & Scrimgeour 1997). Therefore, plant $\delta^{15}\text{N}$ may vary according to species, time of year, stage of plant maturation or which plant part is analysed (Handley & Scrimgeour 1997). However, nitrogen isotopes have a role in indicating the trophic level of organisms during carbon isotope analysis. Assimilation by animals does not alter $\delta^{15}\text{N}$ of a nitrogen source, but subsequent greater excretion of $\delta^{14}\text{N}$ in urine leads to an increase in $\delta^{15}\text{N}$ of animal tissue relative to the source (Peterson & Fry 1987). A review of the results of 22 studies showed that changes in $\delta^{15}\text{N}$ ranged from -0.7 to $+9.2\text{‰}$ between trophic levels with a mean of $2.92 \pm 1.78\text{‰}$ (1SD) (Vander Zanden 2001). Comparison of $\delta^{15}\text{N}$ values of consumers and producers can then suggest whether the consumer is a herbivore, first level carnivore, or higher up in the food chain.

1.7.3 Using stable isotopes to trace the fate of carbon derived from aquatic macrophytes

Recent stable isotope studies of tropical floodplain systems support the view that macrophyte carbon does not enter aquatic food webs in significant volumes. For example, Lewis *et al.* (2001) combined stable isotope studies with calculations of floodplain productivity in the Orinoco River to show that 98% of floodplain production could be attributed to macrophytes and tree leaf litter, but fish and invertebrate carbon isotopes indicated a phytoplankton-dominated diet. Similarly, carbon isotope ratios of detritivorous fish (Characiformes) in the Amazon were too depleted in the heavy isotope for anything other than phytoplankton to be the food source (Araujo-Lima *et al.* 1986). C_3 macrophyte carbon may also have been important to some species but overlapping $\delta^{13}C$ values made it difficult to quantify this. Bunn & Boon (1993) similarly found very ^{13}C depleted consumers in three Australian billabongs, and despite sampling terrestrial, emergent, floating and submerged macrophytes, and filamentous algae and planktonic cyanobacteria, they could not find a potential carbon source.

The source of carbon supporting commercially important fish stocks is of interest due to the need to understand and manage fisheries (Benedito-Cecilio *et al.* 2000; Benedito-Cecilio & Araujo-Lima 2002). However, it appears that the most abundant fish do not derive much carbon from the plentiful supply of aquatic macrophytes in the Amazon and Orinoco Rivers (Araujo-Lima *et al.* 1986; Hamilton, Lewis & Sippel 1992). The sink for this substantial carbon source remains unclear and so it is necessary to turn the focus away from fish in order to understand the role of macrophytes, if any, in supporting floodplain food webs.

The consumption of necromass or detritus by invertebrate detritivores, such as the Oligochaeta and chironomid larvae which dominate the benthic invertebrate fauna of the Upper Rio Paraná floodplain (Takeda, Shimizu & Higuti 1997), is an alternative pathway by which carbon may be assimilated into aquatic food webs. Direct grazing of epiphytic algae or macrophyte tissue itself by invertebrates could also be a significant route of carbon transfer. However, Hamilton, Lewis & Sippel (1992) showed that $\delta^{13}C$ of invertebrates living in association with isotopically distinct aquatic macrophytes did not reflect macrophyte $\delta^{13}C$. Instead, all of the species shared $\delta^{13}C$ values distinct from the plants, suggesting that their host plants were not providing a source of food. This study aimed to investigate these alternative pathways of carbon entrance into the floodplain food

webs of the Rio Paraná using stable isotopes (^{13}C and ^{15}N) and focusing on the movement of carbon through detritus, to sediments and finally to primary consumer invertebrates.

1.8 Meeting the aims of the project

Central to this study were the surveys of vegetation and environmental characteristics of aquatic, terrestrial and transitional habitats of the Paraná floodplain near Porto Rico. These produced extensive data sets which helped to reveal the types of vegetation-environment relationships structuring the floodplain plant communities. To complement this investigative approach, three aspects of the functioning of floodplain vegetation were chosen for closer study. These were the impacts of livestock grazing on wetland and island vegetation, competitive interactions between pairs of free-floating aquatic plant species and the role of aquatic macrophytes in contributing carbon to aquatic food webs.

These approaches were intended to answer the aims of the study, firstly by providing descriptions of the floodplain vegetation in the form of information about patterns in species distributions and collective vegetation structure in relation to the environmental factors influencing them. A major human impact on the vegetation of drier areas was addressed through grazing experiments, and the importance of biotic factors as well as environmental factors in structuring aquatic plant communities through competition experiments. The stable isotope study took a single potential role of macrophytes in floodplain functioning, the provision of a carbon source, and attempted to evaluate this.

The identification of factors involved in regulating the floodplain vegetation is critical in order to allow effective management of the system and thereby to achieve the goals of maintaining biodiversity, conserving habitats which no longer survive elsewhere on the Paraná and allowing the human population to utilise floodplain resources in a sustainable way.

2 Aquatic vegetation of the Upper Paraná River floodplain near Porto Rico

2.1 Aims

- To describe the vegetation of the aquatic habitats of the study area by its species assemblages, by its physical structure and by the morphological traits of the dominant species.
- To identify relationships between these vegetation characteristics and environmental gradients in the floodplain.
- To test these relationships using a test data set including new independent sampling sites and repeat sites.

2.2 Introduction

As a protected area (Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná) of value both for biodiversity conservation and natural resources, the Porto Rico section of the Paraná River floodplain requires careful management. It is therefore essential to understand the factors driving its functioning. The aquatic environments currently support a large number and wide diversity of organisms and have in the past provided an important fishery resource. By investigating the relationships of vegetation structure and species composition and diversity with environmental gradients, understanding of how the system currently functions may be increased. This would allow consequences of changes in environmental conditions for vegetation communities and the organisms that they support to be better anticipated. This information may be helpful in the development of management policies to ensure that the floodplain continues to perform its biodiversity support role. Management aiming to restore suitable habitat conditions for the recovery of fish populations could also help to improve the value of the floodplain as a fishery once again.

The results of two seasons of vegetation and environment surveys conducted in the aquatic habitats of the study area are presented in this chapter. Three major plant community types identified by the use of cluster analysis are compared and their associations with different environmental conditions are described. This classification process much simplifies a very

large, multivariate dataset and helps to identify broad patterns that correspond to large-scale variations in the aquatic habitats. Defining vegetation communities provides a basis for monitoring sites for changes in community type that would indicate significant changes in the local environment.

The variation in species compositions across the sample sites is illustrated in ordination diagrams and patterns in the data are related to gradients of environmental factors and vegetation structure. This analysis is perhaps more realistic than the classification analysis because species compositions are ordered along continua (the ordination axes) reflecting the more subtle variations between sites. The roles of several environmental variables in determining species composition may be interpreted. If sites are sampled repeatedly, then any migration of site points in the ordination diagram over time may indicate which environmental factors are changing at the site and in what way.

Relationships between physical properties of the vegetation and predictive environmental variables are described by regression equations. Such relationships provide very specific information on the likely outcome of future changes in the predictive variables and so could be very useful if management is focused on a particular vegetation property, such as species richness or biomass.

The stability of patterns in vegetation and environment characteristics detected during these analyses is assessed by comparing them with a small test data set. Patterns in the two-year data set are of interest in themselves, but to have a predictive value it is important that they also fit data collected from independent sites.

Some species did not respond strongly to habitat variations with changes in abundance and tended to occur in more than one community type. Examination of four years' of species data (1998-2001) showed that *Eichhornia azurea* and *Eichhornia crassipes* were widespread in the floodplain and were components of more than one vegetation community. *E. azurea* was the most frequently recorded dominant species (Figure 2.1), followed by *E. crassipes*. This was despite wide-ranging physical and chemical properties of the waterbodies themselves, and variation in the plant communities which they supported.



Figure 2.1 Surveying *Eichhornia azurea* dominated vegetation at Curutuba Canal (Steve Roemmele, GU Expedition 2001).

Environmental gradients in the floodplain result from variations in topography and the effect of the Paraná River and its tributaries, which influence water chemistry and water table level during flood events (Thomaz, Roberto & Bini 1997; Junk, Bayley & Sparks 1989). However, increasing disturbance of the river's natural hydrological cycle by upstream dams (Agostinho & Zalewski 1996) has led to alterations in aquatic communities (Agostinho *et al.* 2000) and biological production and successional processes (Thomaz, Roberto & Bini 1997; Ward & Stanford 1995). Such natural and human-induced influences on floodplain environments have consequences for growth patterns of aquatic macrophytes (Benassi & Camargo 2000; Rubim & Camargo 2001). The importance of the two *Eichhornia* species across the range of habitats found in the Paraná illustrates their plasticity and ability to adapt to different growth conditions (*e.g.*, Camargo & Esteves 1996; Gopal 1987). For example, *E. crassipes* is a component of every one of the Paraná floodplain aquatic plant community types discussed by Neiff (1986) while *E. azurea* occurs in all but one. As conditions vary across the floodplain due to both natural processes and anthropogenic impacts, it is interesting to investigate how *E. azurea* and *E. crassipes* respond to different habitat types by analysing their morphological responses to vegetation type and environmental factors at locations where their success is indicated by their predominance in the plant community. Their relationships with environmental conditions are therefore investigated by analysis of morphological trait data collected between 1999 and 2001.

2.3 Methods

2.3.1 Field survey methods

Selection of sites

Field surveys were conducted in a variety of floodplain habitats during spring 2000 (September – November) and 2001 (August – September). Sampling sites were selected to include examples of each of the following categories of waterbody found in the floodplain: main channels; backwaters and open lagoons connected to main channels; canals flowing between main channels; closed (*i.e.*, not connected to a river) várzea lagoons; closed, temporary (*i.e.*, tend to dry up during dry season) island lagoons (Table 2.1, Figure 2.5). The sites had at least two types of vegetation present in a zonation from aquatic to terrestrial habitats and in most cases were structured in three sections; aquatic macrophytes (aquatic sub-sites, A, *e.g.*, Figure 2.2), bank or shore vegetation (bank sub-sites, B, *e.g.*, Figure 2.3) and thirdly terrestrial or wetland vegetation (floodplain sub-sites, C, *e.g.*, Figure 2.4). In 2000 the sites were associated with the Paraná and Baía Rivers and in 2001 with the Paraná, Baía and Ivinheima Rivers. The sites covered a range of human uses of the floodplain and its islands, with some located in areas used for fishing and cattle raising of various intensities, while others consisted of relatively natural, undisturbed vegetation. The aquatic environments associated with the unregulated Ivinheima River can be considered closest to a natural state. However, these undisturbed sites were still potentially vulnerable to grazing, trampling and fishing by the indigenous animals, including deer, capybara and caiman.



Figure 2.2 Porto Rico Island, sub-site A, a temporary lagoon, September 2000.



Figure 2.3 Porto Rico Island, sub-site B, the lagoon shore, September 2000.



Figure 2.4 Porto Rico Island, sub-site C, a levee separating the lagoon from the river, September 2000.

The sites sampled in 2000 and 2001 differed in location and waterbody type for practical reasons and due to variations in the study site. In 2000, all of the sites sampled were associated either with the Paraná River or the Baía River because they were relatively close to the field station and therefore easier to sample. A significant proportion of the nearby waterbodies were temporary island lagoons. The more distant Ivinheima River was not sampled due to time and resource limitations. University of Maringá students provided assistance in the field and laboratory in 2000. The Ivinheima River was sampled in 2001 when the Glasgow University Brazil Expedition team provided assistance. The exceptionally low river level in 2001, due both to a lack of rainfall in the upstream states and to the retention of floodwaters in Porto Primavera reservoir, meant that most temporary lagoons had dried out while other potential sites had become inaccessible by

boat. This further influenced the selection of sites. Lastly, only one site on the main channel of the Paraná was sampled in 2000 and, because both its vegetation and environmental characteristics were very different from the other sites, it was decided to collect further data on this habitat type by selecting more sites in the main channel in 2001. In 2002, sampling at three sites that had been surveyed in the previous two years was repeated. Ten new sites were also sampled comprising two Paraná River backwaters, four Paraná River island lagoons, one main channel Paraná River site, one Baía River open lagoon, one Ivinheima River open lagoon and one Ivinheima River channel site.

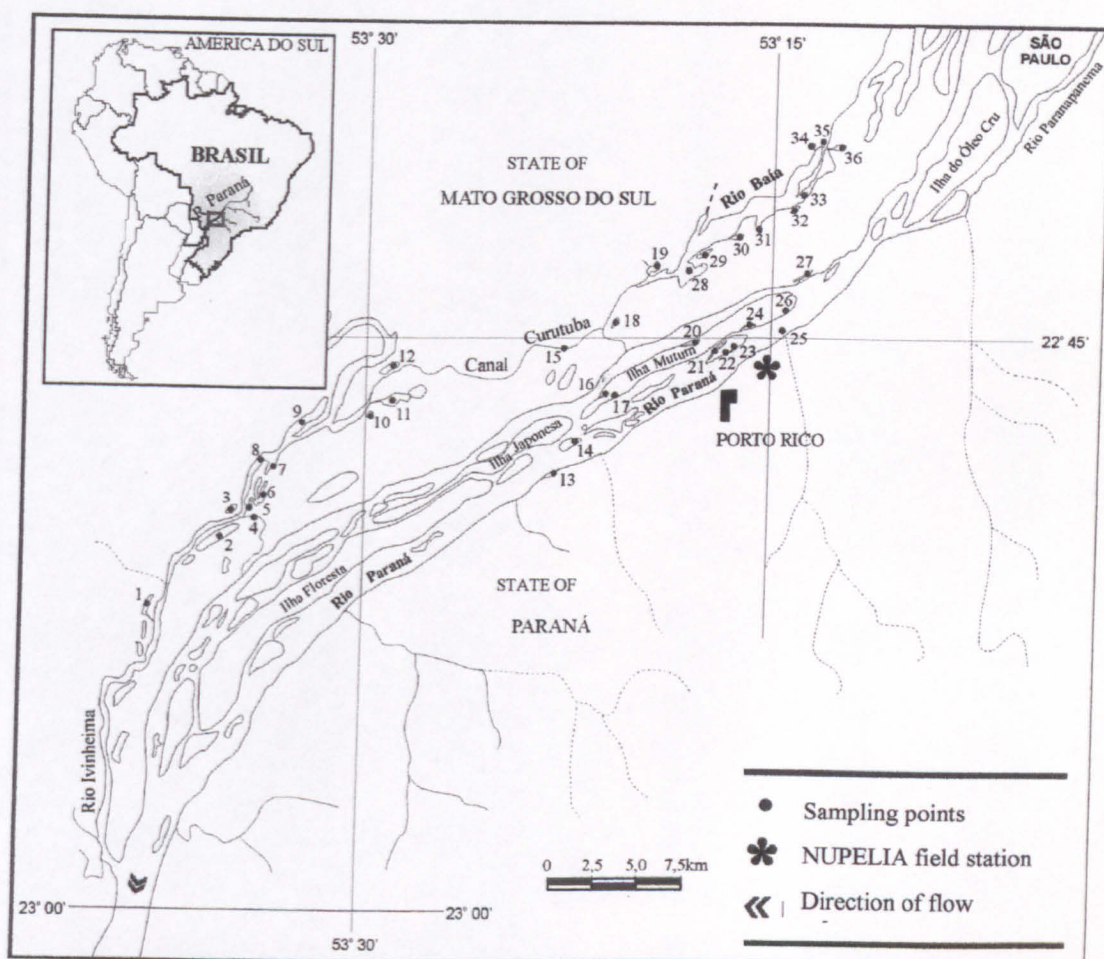


Figure 2.5 Map of the study area showing the three principal rivers, Paraná, Baía and Ivinheima. The numbers indicate sampling stations involved in a long-term monitoring project (PELD) being carried out by researchers at NUPÉLIA. Several of these sites were also sampled during surveys conducted for this thesis: 1. Lagoa Peroba (PER); 2. Lagoa Ventura (VEN); 5. Lagoa Boca do Ipoitã (IPO); 6. Lagoa dos Patos (PAT); 9. Lagoa Finado Raimundo (FRA); 10. Lagoa do Jacaré (JAC); 11. Lagoa Sumida (SUM); 13. Canal Cortado (COR); 14. Lagoa das Pombas (LDP, POM); 15. Canal Curutuba (CUR, 2,3); 16. Ressaco do Manezinho (MAN); 17. Lagoa do Osmar (LOS); 18. Lagoa da Traíra (TRA); 19. Lagoa do Guaraná (GUA); 20. Ressaco do Bilé (BIL); 21. Ressaco do Leopoldo (LP, LP2); 24. Ressaco do Pau Véio (PVF, 2, RIM); 26. Lagoa Pousada (POU); 27. Lagoa das Garças (LGA); 29. Lagoa Fechada (FEC); 30. Lagoa Pousada das Garças (PGA); 31. Lagoa dos Porcos (POR); 34. Lagoa Maria Luiza (MLA, 2); 36. Lagoa da Onça (ONC).

Table 2.1 Sites sampled during Spring 2000, 2001 and 2002 and codes used in ordination diagrams. Sub-site codes A: aquatic, B: bank or shore (B1: temporary bank, B2 permanent bank), C: adjacent floodplain vegetation.

Site name	Location	Waterbody type	Year	Code	Sub-sites sampled
Porto Rico Island	Paraná island	Temporary lagoon	2000	PR	ABC
Ressaco do Leopoldo	Paraná River	Backwater	2000, 2001, 2002	LP, LP2, LP3	ABC, AB2C, ABC
Boca da Jandina	Baía River	Main channel	2000	BJ	ABC
Sete Figueiras	Baía River	Main channel	2000	SF	ABC
Lagoa Preto	Paraná island	Temporary lagoon	2000	TO	ABC
Lagoa Carioca	Paraná island	Temporary lagoon	2000	CAR	ABC
Lagoa Carioca	Paraná island	Temporary lagoon	2002	CAR2	ABC
Lagoa do Osmar	Paraná island	Temporary lagoon	2000	LOS	ABC
Lagoa dos Porcos	Baía River	Connected lagoon	2000	POR	ABC
Lagoa Pousada	Paraná island	Temporary lagoon	2000	POU	ABC
Lagoa das Garças	Paraná River	Connected lagoon	2000	LGA	ABC
Lagoa das Pombas	Paraná River	Connected lagoon	2000	LDP	AB
Lagoa das Pombas	Paraná River	Connected lagoon	2001	POM2	AB1B2C
Lagoa Fechada	Baía River	Várzea lagoon	2000	FEC	ABC
Lagoa Maria-Luiza	Baía River	Connected lagoon	2000	MLA	ABC
Lagoa Maria-Luiza	Baía River	Connected lagoon	2001	MLA2	AB1B2
Canal Cortado	Paraná River	Connecting channel	2000	COR	ABC
Canal Cortado	Paraná River	Connecting channel	2001	COR2	AB1B2C
Canal Curutuba	Baía / Ivinheima	Connecting channel	2000, 2001, 2002	CUR, CUR3, CUR4	ABC, AB2C, ABC
Canal Curutuba	Ivinheima / Baía	Connecting channel	2001	CUR2	AB2C
Entrada do Baía	Baía River	Main channel	2000	EDB	ABC
Baía floodplain	Baía River	Main channel	2000, 2001, 2002	BFP, BFP2, BFP3	ABC, AB2C, ABC
Ressaco do Pau Véio	Paraná River	Backwater	2000	RIM	ABC
Ressaco do Pau Véio	Paraná River	Backwater	2000, 2001	PVF, PVF2	ABC, AB1B2C
Rio Paraná bank	Paraná River	Main channel	2000, 2001	RPM, RPM2	ABC, AB2C
Rio Paraná bank	Paraná River	Main channel	2002	RPM3	ABC
Ivinheima channel	Ivinheima River	Main channel	2001	IVI	AB1C
Ivinheima channel	Ivinheima River	Main channel	2002	IVI2	ABC
Lagoa dos Patos	Ivinheima River	Connected lagoon	2001	PAT	AB2C
Lagoa da Onça	Baía River	Connected lagoon	2001	ONC	AB2C
Lagoa Carão	Baía River	Connected lagoon	2001	CRO	AB1C
Lagoa do Guaraná	Baía River	Connected lagoon	2001	GUA	AB1C
Lagoa Boca do Ipoitã	Ivinheima River	Connected lagoon	2001	IPO	AB1C
Lagoa Sumida	Ivinheima River	Connected lagoon	2001	SUM	AB2C
Lagoa Peroba	Ivinheima River	Connected lagoon (disconnected)	2001	PER	AB1B2
Lagoa Ventura	Ivinheima River	Várzea lagoon	2001	VEN	AB2C
Ressaco do Bilé	Paraná River	Backwater (disconnected)	2001	BIL	AB1B2C
Lagoa da Traira	Baía River	Várzea lagoon	2001	LATR	AB2C
Paraná Islands	Paraná River	Main channel	2001	ISL	AB1B2C
Capybara lagoon	Baía River	Bay in channel	2001	CAP	AB1B2C
Lagoa do Geraldo	Paraná Islands	Temporary lagoon	2001	GER	AB1B2C
Lagoa do Zé Marim	Paraná Islands	Temporary lagoon	2002	ZEM	ABC
Lagoa do Cidão	Paraná Islands	Temporary lagoon	2002	CID	ABC
Lagoa do Tião	Paraná Islands	Temporary lagoon	2002	TIA	ABC
Lagoa do Finado	Ivinheima River	Connected lagoon	2002	FRA	ABC
Raimundo					
Jacaré lagoon	Curutuba channel	Várzea lagoon	2002	JAC	ABC
Ressaco do Manezinho	Paraná River	Backwater	2002	MAN	ABC
Pousada das Garças	Baía River	Bay in channel	2002	PDG	ABC

Field Sampling

Species frequency

At each site, two or three sub-sites were sampled depending on whether two or three zones of vegetation could be identified. At each sub-site, a 1m² quadrat (subdivided into 25 0.2m x 0.2m squares) was placed at three random locations and used to measure the frequency of species by counting the number of squares in which each species was present.

Collective vegetation variables

The measurement of collective vegetation variables, also known as vegetation state variables, further simplifies vegetation description. These values provide an overall measurement of all individuals in a particular vegetation type regardless of species. The variables measured in this study were canopy height, percentage canopy cover, stem density and biomass. Previous studies have found these variables to be related to other environmental and biotic factors in the aquatic habitats of the floodplain (Murphy *et al.* 2003). Similarly, Willby, Murphy & Pulford (1998) showed that wetland plant diversity in a Scottish floodplain could be predicted from measurements of vegetation state variables, although they pointed out that environmental variables are better predictors as they are the underlying drivers of plant community functioning.

Within each 1m² quadrat, three variables were measured at three randomly selected points for the vegetation as a whole. These were canopy height, stem density in a 0.1m x 0.1m quadrat (or larger if necessary due to vegetation structure), and percentage canopy cover in a 0.1m x 0.1m transparent, plastic, sub-divided quadrat. In the case of free-floating aquatic plants, each floating unit was counted as one stem. A figure for percentage canopy cover was obtained by holding the 0.01m² quadrat above the vegetation and estimating, with the help of the sub-divisions, the proportion filled by any part of a living plant.

At each sub-site, two randomly located biomass samples were taken using a quadrat of a size suitable to the type of vegetation, frequently 0.5m x 0.5m, or 0.2m x 0.2m, as appropriate (Figure 2.6). Senescing plant parts attached to live plants were included in the biomass sample but detached litter was not collected.



Figure 2.6 Collecting an aquatic biomass sample from Canal Curutuba (CUR), November 2000.

Environmental variables

At aquatic sampling points, underwater light attenuation, water pH, water conductivity and sediment redox potential were measured. Light attenuation was measured using a twin-sensor SKYE SKP210 system. The hand-held light meter was connected to two sensors of photosynthetically active radiation (PAR) that were taped to a metre stick. One sensor was held at the water surface and the other at a measured distance below the surface. PAR incident to the two sensors was recorded at least three times and the mean values used to calculate light absorption in the water. Water pH and sediment redox potential were both measured using a hand-held Hanna pH and redox meter with the relevant electrode attached. Water electrical conductivity was measured using a hand-held Hanna conductivity meter. Water depth was measured in the middle of each 1m² quadrat. A water sample was taken for later laboratory analysis of total organic nitrogen and total phosphorus. At each sub-site, a soil or sediment sample was collected for pH measurement and later laboratory analysis of phosphorus, nitrogen, calcium and iron content.

Dominant species trait measurements

A sample of the dominant species (the species with the highest frequency over the three quadrats) was collected for measurement of morphological traits comprising stem length, leaf area, leaf weight, root weight, remainder weight (stem plus any remaining structures *e.g.*, flowers) and total plant weight. These six different traits were chosen for measurement based on those found in previous work (Murphy *et al.* 2003) to be useful predictors of species diversity in conjunction with environmental variables. In the case of colonial plants, such as *E. crassipes*, a single colonial individual was collected. *E. azurea*

is bank-rooted with floating stems which reach out several metres into the water with roots and emergent leaves at each node. Samples were taken from this species by counting back ten leaf-nodes (2000 and 2001 average sample length 1.45m) from the distal end of the stem and cutting off the specimen at this point.

Morphological trait measurements of dominant species are likely to reflect the ecological functioning of a population of a particular species because traits potentially involved in resource capture, disturbance tolerance and competitiveness contribute to plant survival and reproductive capacity. Intuitively, the dominant species is that which is best adapted to local conditions of stress, disturbance and competition, the three primary constraints on plant survival identified by Grime (1977). The relationship between sets of plant trait measurements and Grime's three primary survival strategies (stress tolerance, disturbance tolerance and competitive ability) has been established for European riverine wetland vegetation (Hills & Murphy 1996; Hills *et al.* 1994). In particular, there are associations between greater plant height and increased competitive ability, and lower dry weight of stems and increased stress tolerance (Hills *et al.* 1994). Plant trait measurements can also be related to habitat properties. Willby, Abernethy & Demars (2000) demonstrated the association of certain field-measured and literature-derived plant attributes with physical features of aquatic habitats.

Plant trait measurements therefore provide indicators of environmental conditions and species diversity and so constitute a potential tool for the detection and prediction of changes in these factors. By describing vegetation in terms of dominant traits rather than species composition, techniques relating vegetation to habitat become more generally applicable. Trait measurements are relatively easy to make and there is less dependence on taxonomic knowledge than in phytosociological studies. In addition, there is less dependence on the presence or absence of a particular species which may have a distribution influenced by factors such as propagule dispersal rather than the physical or chemical suitability of a colonisation site.

Site details

Grazing intensity, shade and the degree of openness were assessed at each sub-site using the five-point scales detailed below. Grazing was considered in the context of anthropogenic disturbance to floodplain vegetation and so grazing damage which appeared to be caused by invertebrates was not evaluated. However, it was not possible to

distinguish whether grazing had been caused by native mammals or by domestic livestock and so the visual assessment scored the combined effect of both groups of grazers.

Grazing intensity:

1 = None; 2 = A little grazing resulting in clipping of some species; 3 = Intermediate degree of grazing resulting in damage to the vegetation and other evidence such as occasional animal droppings; 4 = More severe damage to vegetation, low-growing plants, droppings; 5 = Intensive grazing resulting in a very short sward height with other evidence of grazing such as cattle droppings at a high frequency or bare ground.

Degree of openness: 1 = No shrubs or trees; 2 = 10% of sky obscured by shrubs or trees; 3 = 50% obscured, e.g., trees all around but some distance away; 4 = 75% obscured, e.g., a clearing in a forest; 5 = No sky visible due to tree and shrub cover, e.g., under dense forest.

Shade: 1 = In full sunlight; 2-4 = Estimated intermediate ratings; 5 = Very low light, e.g., under forest canopy.

Laboratory work***Collective vegetation variables***

The biomass samples were dried and weighed and the dry weight biomass per square metre was calculated. All samples for which dry weight was to be measured were dried to constant weight in an oven heated from below by rows of light bulbs.

Environmental variables

Water samples were frozen as soon as they could be delivered to the field station, usually around midday following the morning in which they were collected. Analysis of water samples for total phosphorus and total organic nitrogen concentrations was carried out by staff of the Nucleus of Researchers in Limnology, Ichthyology and Aquaculture (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, NUPELIA) at the State University of Maringá (Universidade Estadual de Maringá, UEM). Water total phosphorus was analysed spectrophotometrically after ascorbic acid digestion and molybdate reaction.

Total organic nitrogen was determined by acid digestion followed by acid steam distillation with a titrimetric finish.

Sediment pH was measured with a Hanna hand-held pH meter as soon as possible after the samples were brought back to the field station. Sediment samples were then dried in an oven before being ground finely (<1mm particle size) using a mortar and pestle.

Soil analyses were carried out by the soil analysis service of the Scottish Agricultural College, Auchincruive, Ayr. ADAS extractable phosphorus was measured by bicarbonate extraction followed by ascorbic/molybdate colorimetric finish and total Kjeldahl nitrogen by catalysed acid digestion followed by steam distillation and titrimetric finish (Ministry of Agriculture, Fisheries & Food 1986). Total calcium and total iron were determined by acid digestion of soil samples followed by Inductively Coupled Plasma Atomic Emission Spectroscopy.

The light extinction coefficient, k , which describes light absorption in the water column, was calculated from the two measurements of PAR intensity taken at each aquatic sub-site.

$$k = -\log_e (\text{PAR}_{\text{depth}} / \text{PAR}_{\text{surface}}) / \text{depth}$$

$\text{PAR}_{\text{depth}}$ = PAR intensity at a measured distance below the water surface, $\text{PAR}_{\text{surface}}$ = PAR intensity at the water surface, depth = depth below the water surface at which underwater PAR was measured.

The value of k can be used to estimate the depth to which plants can be expected to have a sufficient supply of PAR for photosynthesis to exceed respiration, permitting plant growth. The depth in the water at which photosynthesis = respiration (the compensation point) is termed the euphotic depth (Z_{eu}) and the part of the water column above this level where net photosynthesis is possible is called the euphotic zone. Z_{eu} for aquatic macrophytes is the depth at which approximately 3% of surface light intensity remains and is estimated by dividing a constant by k (Moss 1998; Sabbatini & Murphy 1996).

$$Z_{\text{eu}} = 3.51 / k$$

The extent of the euphotic zone relative to the total water depth (Z_{eu}/d) indicates the proportion of the water column that is potentially suitable for submerged plant growth. Both Z_{eu} and Z_{eu}/d were calculated for each aquatic sub-site.

Dominant species trait measurements

On returning to the laboratory, the plants were washed and the maximum stem length from the tip of the longest leaf to the base of the stem was measured. A sample of approximately five leaves was taken and these were flattened as much as possible and scanned for leaf area using a portable "Scanman" scanner and "Paint Shop Pro 5". The area of the images was calculated using "Delta-T-Scan" software on a laptop computer. This sub-sample of leaves was then dried and weighed. The roots, stem and residual leaves of the rest of the plant were separated and also dried and weighed to give the dry weight of the individual components per plant. The ratio of the weight of the leaf sub-sample to the total leaf weight (sub-sample + residual leaves) was used to estimate the total leaf area of the plant from the area of the sub-sample. From the weight of the individual components, the whole plant dry weight was calculated.

Species Identification

At each site, samples of the unknown species were collected and preserved by pressing and drying. These were stored in the NUPELIA herbarium at UEM and later identified as far as possible with the help of staff at NUPELIA following Cook (1990a), Cook and Urmikönig (1984), Hoehne (1979), Junk (1986), Lowden (1986), Neiff (1986), Thomaz *et al.* (2004) or Velasquez (1994) where appropriate. Authorities were confirmed using the W³TROPICOS database accessed through the Missouri Botanical Garden website (www.mobot.org).

2.3.2 Data analysis

TWINSPAN methods

TWINSPAN (two-way indicator species analysis) (Hill 1979) is a technique for the reduction and exploration of species data sets through classification of samples. It is a polythetic divisive classification method meaning that it uses all of the species data to make a dichotomy in a set of samples to form two groups, then splits these groups into pairs of smaller groups and continues this process until groups reach a minimum size set at the beginning of the analysis. It is superior to earlier techniques, such as association analysis, which uses only the presence or absence of single species to differentiate groups, because it makes use of abundance data of all species. Abundance information is converted to a qualitative form by the use of pseudospecies. There are a number of possible pseudospecies per species, each representing the presence of that species within a

particular range of abundance. Each pseudospecies can then be either present or absent (a qualitative measure) representing the abundance at which a particular species occurs (a quantitative measure). Pseudospecies are cumulative and not exclusive because a sample containing a species in high abundance may be recorded as having all the pseudospecies for that species present, while a sample with that species at low abundance will only have the low abundance pseudospecies.

The analysis involves an initial division of samples using ordination followed by refinement of the position of the dichotomy using indicator species. First, pseudospecies are derived from the species data according to the abundance of each species. The raw species data are ordinated and the ordination space partitioned by dividing the first axis at the centroid, forming two groups. Each pseudospecies is assigned a positive or negative indicator value which is a measure of its tendency to occur on one side of the division or the other. Samples are then allocated indicator scores based on the number of negative and the number of positive indicators they include. These indicator scores are used to make an alternative dichotomy in the samples. The threshold indicator score for identifying the position of the division is set at a level which makes this second classification agree most closely with the primary ordination. This step therefore refines the primary ordination using indicator scores. Final adjustments are made to the position of the division in the primary ordination in order to minimize discrepancies between classifications obtained through the primary ordination and the refined ordination. The process is repeated at each level of the classification until groups become too small for further division to be ecologically significant.

The output of the TWINSpan analysis is summarised in a two-way ordered table which clearly shows where divisions have been made. It arranges samples so that those which are most similar are placed close together in the table while those which are least similar are further apart. Similarly, species likely to co-exist are close together in the table while those which are unlikely to occur together are further apart. Indicator species and preferential pseudospecies are also recorded.

TWINSpan analysis was used to assist with the interpretation of species abundance data collected during the surveys conducted in 2000 and 2001. The data from each year was first analysed separately and then combined to give a large data set of information on a greater variety of habitats in the floodplain. The aquatic species data inputs for the TWINSpan programme consisted of a matrix of 20 sites and 27 species in 2000, 23 sites and 21 species in 2001 and 43 samples and 30 species when combining the data from both

years. Cut levels for pseudospecies were set at 0.1, 4.0, 8.0, 15.0. This represents four possible pseudospecies for each species present, *i.e.*, present at an average frequency of between 0.1 and 3.9 squares per quadrat, between 4.0 and 7.9 squares per quadrat, between 8.0 and 14.9 squares per quadrat, and 15.0 squares or more per quadrat. The minimum group size for division was set at six with a maximum number of five divisions to avoid re-expansion of the data set to its original form. The outputs from the analysis were examined and ecologically relevant vegetation types identified. TWINSpan analysis was conducted using the Vespan programme.

The distribution of plant species in the floodplain waterbodies is controlled by complex factors which determine whether or not a particular individual successfully colonises any particular growing site. These include the range of light, water depth and flow, water and/or sediment chemistry and disturbance conditions to which the species is adapted, as well as its ability to compete with other plants and chance factors, such as the likelihood of its propagules reaching a particular habitat in the first place. Therefore, it can be anticipated that vegetation communities are reflecting the biotic and abiotic conditions in existence where they are growing. The TWINSpan groups collect together sites that are similar in their species composition and separate those which are very different. It is likely that there are underlying factors controlling the species assemblage at each site, which can be expected to be more similar within groups than between groups. Comparison between groups of environmental and vegetation characteristics may help to explain what is controlling vegetation types. Understanding the factors that influence vegetation communities provides a key to their management for a particular purpose whether that is to support threatened organisms or to provide an economically useful vegetation resource.

Environmental, vegetation and dominant trait variables collected at the sites were compared between the groups. Each variable was tested for normality and equal variance between groups and transformed if necessary by taking the square root or natural logarithm. One-way ANOVA and Tukey's multiple comparisons were used to compare variables that were normally distributed and had equal variance between groups. Kruskal-Wallis tests followed by an alternative multiple comparison procedure (Siegel and Castellan 1988) were used to compare variables which did not satisfy the assumptions of ANOVA. Differences between TWINSpan groups were considered significant if $p \leq 0.05$. These procedures were carried out using Minitab 13.3.

Ordination methods

Ordination analysis includes a number of methods which produce graphical summaries of species data resulting from field surveys. The depiction of survey data within a space defined by two major axes simplifies the process of identifying patterns in species distribution and abundance and interpreting these in relation to environmental gradients. Detrended correspondence analysis (DCA) (Hill & Gauch 1980) and canonical correspondence analysis (CCA) (ter Braak 1986) are the two methods used in this chapter. Both DCA and CCA assume that the abundance or frequency of occurrence of species responds unimodally in relation to the environment, in contrast to other techniques which assume a linear response. DCA is based purely upon the species data but the output can be interpreted in light of any additional available data. CCA has both species and environmental data as its input and aims to detect patterns in the species data that can be explained by the environmental data provided.

The results of DCA and CCA of the three data sets (2000, 2001 and combined 2000-2001) were discussed and compared. The validity of conclusions drawn from these analyses was assessed by testing the fit of the additional independent data set collected in 2002.

The ordination techniques referred to in this chapter are described by Jongman, ter Braak & van Tongeren (1995). CANOCO 4 (ter Braak & Šmilauer 1998) was used to perform the DCA and CCA analyses.

DCA

The diagrams generated by DCA consist of points representing sites or species ordinated in a two-dimensional space according to their scores on two ordination axes. The relative positions of the points indicate the degree of similarity between them so that sites that are close together can be expected to have similar species assemblages and species that are close together can be expected to co-occur.

DCA involves the construction of artificial gradients which best explain the observed species distributions and can be considered to integrate a real underlying set of abiotic, biotic and chance factors which determine the success of different species. These gradients are the axes of the ordination diagrams.

On a real environmental gradient, each species can be expected to have a niche which is the range of conditions in which it can survive. Within this niche, there will be an

optimum value at which the species can be expected to grow best and reach highest abundance. Abundance is expected to vary unimodally about this optimum, decreasing as conditions become less ideal for growth in both directions on the gradient.

If a set of species has well dispersed optima on this gradient, the value of the variable at any particular site will be important in determining which species are present or abundant and which are not. This variable explains the species distribution well. If the optima are close together on the gradient, many or all of the species may be able to tolerate the value at a particular site and so the variable will not help to explain the presence or absence of the species.

DCA aims to construct a gradient that maximises the dispersion of the optimum values for the species and therefore gives the best possible explanation of the observed species distribution. It does this with a two-way weighted averaging algorithm. This is based on the assumption that the optimum position on an environmental gradient for a particular species can be deduced by calculating the mean value of that variable across all of the sites where that species grows, weighted by its abundance at each site. Sites with highest abundance of the species are likely to have values of the variable closest to the species optimum while sites with low abundance can be presumed to have values further from the optimum. In reverse, it should be possible to estimate the value of an environmental variable at a particular site by calculating the average of the optimum values of that variable for the species growing at that site, weighted by their abundances. The species with optima closest to the site conditions should be in greatest abundance while those with optima more distant from the site value will probably be in low abundance.

DCA begins by assigning arbitrary values, representing scores on an artificial gradient, to the sites. These are called the site scores. These site scores are then used to calculate species scores as described above. For each species in turn, the average of the site scores across all of the sites where the species grows, weighted by its abundance at each site, is calculated. This weighted average is the species score and can be interpreted as the optimum value on the artificial gradient for that particular species.

Each site now has an assemblage of species, each with a species score on the artificial gradient. A new set of site scores is calculated by taking the average of the species scores weighted by the abundance of each species. The new site scores are then used to calculate new species scores and the process is repeated over and over again. With each iteration of the algorithm, the dispersion of the species scores along the artificial gradient increases

until it reaches a maximum. The best artificial gradient for explaining the species data has been extracted and is independent of the initial arbitrary site scores. This is the first ordination axis and the maximised dispersion of the species scores is described by its eigenvalue. The eigenvalue measures how well the artificial gradient, the axis, explains the species data. It may have a value between 0 and +1. When the eigenvalue is close to 0, it indicates that there was little success in constructing an artificial gradient to explain the species data, while if it is close to 1, the ordination axis is explaining the species data very well. Further ordination axes, uncorrelated with earlier axes, are subsequently extracted from the remaining unexplained variation in the species data.

To prevent the range of the site and species scores from becoming smaller and smaller during averaging, they are rescaled. However, this rescaling affects the ordination diagram so that the spread of the scores along the axes does not reflect the importance of each axis in explaining the species data. To overcome this problem, Hill's scaling, which expresses the axis scores in units of standard deviations of species turnover, can be applied.

A potential problem in correspondence analysis (CA) (Hill 1974) is the arch effect. This is a mathematical artefact which results in axis two being quadratically related to axis one so that the scatter of points may have an arch shape. Detrended correspondence analysis (Hill & Gauch 1980) corrects this problem by adjusting site scores on subsequent axes to ensure that their mean value is approximately zero at any point on axis one (Jongman, ter Braak & van Tongeren 1995, p.106). For the detrending by segments method, axis one is divided into segments. The mean value of axis two site scores within each segment is calculated and then subtracted from each of the site scores.

DCA analysis of 2000-2001 species data

Sites by species abundance matrices were constructed from the survey data collected in 2000 and 2001 and from the combined 2000-2001 data set. Preliminary correspondence analyses showed the arch effect occurring in each case. DCA was therefore applied to each data set with detrending by segments. The length of the gradient on axis one was greater than three standard deviations in all analyses indicating that the unimodal method of DCA was appropriate (ter Braak & Šmilauer 1998, p.37). The data were not transformed but rare species were downweighted to reduce their influence on the ordination. Following initial analysis of all sites, some outlying sites were made supplementary (excluded from the process of constructing the axes) to allow relationships between the remaining, less extreme sites to be examined.

Although a DCA ordination is based purely upon species data, the outcome of the analysis can be interpreted in relation to environmental factors which may be responsible for the observed patterns in species distribution, and to physical attributes of the vegetation which may reflect their adaptations to particular habitat conditions. This was done by calculating Spearman rank correlation coefficients between site scores (on axes one and two) and environmental, vegetation and dominant species trait variables (Jongman, ter Braak & van Tongeren 1995, p.132). Correlations were considered statistically significant if $p \leq 0.05$. This process of indirect gradient analysis provides an indication of the predictive importance of environmental factors in explaining the distributions of plant communities and of individual species.

CCA

In DCA, the axes are extracted from the species data in such a way as to best explain the distribution of species across the sites. In order to identify the presumed underlying environmental gradients, relationships between the axes and a set of measured environmental variables can be investigated after the DCA has been completed. This approach suggests the variables that could be causing the main patterns in the DCA diagrams. CCA is useful because it aims to detect any variation in the species data that can be explained by the environmental data, even if this is not the main variation (Jongman, ter Braak & van Tongeren 1995, p.136-137). It is unlikely that species distribution is dictated by a single environmental variable and so CCA helps to identify all those variables which may be playing a part. Rather than trying to match single environmental variables to the species data following DCA, the axes of CCA are formed from a linear combination of the measured variables and therefore may be more likely to explain the species data.

In order to obtain these axes, the DCA algorithm is modified by addition of a regression step. After each new set of site scores is produced by weighted averaging of the species scores, a multiple regression is performed to explain these site scores using the measured environmental variables. The fitted values of this regression are a linear combination of the environmental variables and form the new site scores for calculation of the next set of species scores. As in DCA, the steps are repeated until the best gradient is constructed for explaining the species data. Further axes, uncorrelated with earlier ones, are extracted from the species and environment data in the same way. The outcome is a direct gradient analysis of the sites by species data which illustrates the relationships between species, assemblages and environmental and vegetation gradients across the study area.

Interpretation of CCA diagrams

Due to the multiple regression step in the CCA algorithm, the position of site or species points in the CCA diagram is related to both species composition and the environmental conditions at the site or the environmental preferences of the species. Arrows plotted on the diagram indicate the direction of gradients in each environmental variable across the diagram. The longer the arrow, the more strongly it is correlated with the CCA axes and therefore the more closely it is related to the ordination. Environmental conditions at a particular site, or preferences of a particular species, can be predicted by projecting the site or species point on to the arrow of each environmental variable. Projection of all points on to an arrow can produce an estimated ranking of the sites or species for that variable (Jongman, ter Braak & van Tongeren 1995, p.141).

Following the analysis, Monte Carlo permutation tests can be applied to the CCA axes to determine whether the species data are statistically significantly related to the environment. A test of the first canonical axis compares the null hypothesis of no significant relationship with the alternative hypothesis that there is a single dominating gradient determining the species-environment relationship. A test of all canonical axes has the more general alternative hypothesis that the species data are related to the environment. In the Monte Carlo permutation test, a test statistic, describing the strength of the species-environment relationship, is defined. The reference distribution of this test statistic is obtained by permuting the samples in the species data to produce a number of new data sets, each of which would be equally likely to arise if the null hypothesis was true. The test statistic of each of these data sets is calculated to give the reference distribution with which the test statistic of the actual data set is compared. For a test at the 5% significance level, 199 permutations are considered sufficient (ter Braak & Šmilauer 1998, p.42).

CCA analysis of 2000-2001 species data

In addition to the sites by species abundance matrices, sites by environmental variables matrices were constructed and provided the input data for CCA. Again the data were not transformed but rare species were downweighted. Some sites were made supplementary to simplify interpretation of the ordination diagrams.

The ordination diagrams were plotted with Hill's scaling focused on inter-sample distances for the site ordinations and inter-species distances for the species ordinations. The spread of the points on the axes therefore reflected their relative importance in explaining the species data. Triplots showing site and species points and environmental gradients cannot

optimally display the relationships between site points and between species points. Scaling was focused on inter-sample distances in these diagrams. The dispersal of the site points on the axes therefore reflected the relative importance of the axes in explaining the species data, while the dispersal of the species points was equal on both axes.

Automatic forward selection was selected to calculate which variables were explaining the greatest amount of variation in the species data.

The statistical significance of the first canonical axis and of all of the canonical axes was tested with Monte Carlo permutation tests set to perform 199 permutations under the reduced model.

Correlation and regression analysis methods

An important aim of collecting the survey data from the Paraná floodplain was to formulate equations for the prediction of vegetation variables such as plant species richness and biomass. Plant diversity has an inherent value, but it also has value as a property of the floodplain necessary for supporting the diversity of other organisms (Takeda *et al.* 2003; Lansac-Tôha *et al.* 2003). Likewise, the distribution of plant biomass is important in the provision of habitats and as a food supply. These are properties which integrate the effects of all natural or human-imposed impacts on the floodplain vegetation, and so are themselves indicators of changes occurring in the system. Identifying factors affecting plant species richness and biomass will help in understanding the controls on habitat structure and food provision for birds and fish in the case of aquatic and wetland sites. In terrestrial sites, the amount and type of vegetation is of particular human interest in relation to its potential use for grazing.

Regression is a technique that describes the relationship of a dependent variable (the response), such as species richness, with one or more independent variables (the predictors), such as the environmental variables measured in the floodplain. It fits a curve to the data and allows prediction of the dependent variable using the independent variables.

In linear regression, the relationship between the predictor variables and the response variable is described by a straight line. Least squares regression is a parametric example, although non-parametric techniques also exist, such as semi-averaging and resistant lines. If a linear, parametric model is to be used to describe a relationship, the data must consist of independent observations with a normal distribution measured on a continuous scale.

The model makes the further assumptions that the relationship is best described by a straight line and not by some other curve, that the extent of deviation of y-values from the regression line (the residuals) is consistent along the length of the line and that the residuals are normally distributed about the line. A linear model fitted using least-squares regression produces a straight-line equation describing the resulting value of y (the response variable) for a given value of x (the predictor variable). The r-value for the regression line (whether based on one or more predictors) shows the strength of relationship between the predictor and response variables. A value close to -1 indicates a strong negative relationship while a value close to $+1$ indicates a strong positive relationship. If the value is closer to 0, then the dependent variable is not responding to the independent variable. The coefficient of determination, r^2 , indicates the proportion of variance explained by the regression and can be adjusted to make it independent of the number of predictor variables. The statistical significance of the regression line, however strong or weak the relationship, is determined by using analysis of variance to compare the amount of explained variance with the amount of unexplained variance.

Correlation and regression analysis of 2000-2001 vegetation and environment data

The potential environmental and vegetation predictor variables and the response variables of interest were all tested for normality using Ryan-Joiner tests (Minitab 13.30). Variables were transformed with square root or natural log transformations as necessary to give normal distributions where possible. Normally distributed variables were analysed for significant Pearson product moment correlation coefficients between pairs of variables. Spearman rank correlation coefficients were calculated for any non-normal variables. Correlations were considered significant if $p \leq 0.05$.

Linear, quadratic and cubic relationships were investigated between pairs of predictor and response variables. Predictor variables were combined using stepwise multiple regression to try to produce more robust predictive models than was possible with any single predictor variable.

The models that explained the greatest amount of variation in the response variables were tested to make sure that they satisfied the assumptions of the linear model. A normal probability plot showed whether or not the residuals were normally distributed about the regression line. A scatter of standardised residuals against fitted values derived from the regression showed whether or not the variance in residuals was reasonably constant along

the regression line. The regression procedures and residual analyses were carried out using SPSS 9.0.0.

The abbreviations for vegetation and environmental variables used in the text and equations are explained in Table 2.2, together with the units in which each was recorded.

Table 2.2 Explanation of abbreviations and units for predictor and response variables.

Abbreviation	Variable	Units
Spp	Number of species per sub-site	
Bio	Biomass	gm ⁻²
Height	Canopy height	m
Cover	% Canopy cover	%
Stem	Stem density per m ²	
lar	Total leaf area per plant	cm ²
SLA	Specific leaf area	cm ² g ⁻¹
lwt	Total leaf dry weight per plant	g
rwt	Total root dry weight per plant	g
rem	Remainder dry weight per plant	g
twl	Total plant dry weight	g
slen	Maximum stem length	m
Depth	Water depth	m
z_{eu}/d	Euphotic depth/water depth	
Con	Water electrical conductivity	µScm ⁻¹
WpH	Water pH	
WN	Water total Kjeldahl nitrogen	µgL ⁻¹
WP	Water total phosphorus	µgL ⁻¹
Redox	Sediment redox potential	mV
SpH	Sediment pH	
SN	Sediment total Kjeldahl nitrogen	mgkg ⁻¹
SP	Sediment ADAS extractable phosphorus	mgkg ⁻¹
Ca	Sediment total calcium	mgkg ⁻¹
Fe	Sediment total iron	mgkg ⁻¹

Model testing using the 2002 data set

TWINSPAN and ordination

The species data for each site sampled in 2002 were compared with the species data of the three TWINSPAN groups derived from the 2000-2001 data set. 2002 sites were assigned to the TWINSPAN group that they fitted best in terms of species assemblage and

abundance. Environmental, collective vegetation and dominant species trait variables which differed significantly between 2000-2001 TWINSpan groups were expected to be similar between each 2000-2001 TWINSpan group and the 2002 sites assigned to that group. Mean or median values were compared between each 2000-2001 TWINSpan group and the corresponding 2002 sites using t-tests or Kruskal-Wallis tests.

The 2002 species data set was added to the 2000-2001 species data set and DCA was run on this whole data set to show where the 2002 sites were located in relation to those previously sampled. The relative positions of sites which were sampled in each of the three years of data collection were discussed.

Regression equations

The regression relationships derived from the 2000-2001 data with the greatest predictive power (highest r^2) were tested with the 2002 data set. The values for each predictor variable were entered into the equations and a predicted value was calculated for each vegetation variable.

Predicted and actual values were compared using correlation analysis (Pearson or Spearman correlation coefficients; correlations considered significant if $p \leq 0.05$) or by assessing the frequency of agreement between values.

2.3.3 Variation in morphological traits of *Eichhornia azurea* and *Eichhornia crassipes*

Data collected during spring 1999 (Murphy *et al.* 2003), 2000 and 2001 from a total of 99 randomly selected sites within the waterbodies of the floodplain were used to investigate morphological responses of *Eichhornia azurea* and *Eichhornia crassipes* to vegetation community type and environmental conditions. Species composition data, environmental factors and dominant species trait measurements were collected as described in Section 2.3.1. Sites included open and closed lagoons, backwaters and flowing channels, located within a radius of approximately 40km of the field station at Porto Rico.

TWINSpan analysis of species presence-absence data collected in 1999 (the largest single-year dataset available) classified sites into groups containing similar species assemblages (Murphy *et al.* 2003). Using analysis of variance, the morphological traits of *E. azurea* and *E. crassipes* were compared between the different vegetation types in which

they occurred as dominant species. Variables were tested for normality using Ryan-Joiner tests and for equivalence of variance in groups and then transformed if necessary.

Variables without a normal distribution were compared between TWINSPAN groups using Kruskal-Wallis tests. Differences were considered significant when $p \leq 0.05$.

Correlation and regression analyses were applied to the three-year data set (1999-2001). Fifteen leaf-node sections of *E. azurea* were collected in 1999 and ten leaf-node sections in 2000 and 2001 so the measurements were standardised by dividing trait measurement values where appropriate by the number of nodes per sample. After transformation to normalise variables as necessary, Pearson product-moment correlation coefficients were calculated between pairs of trait and environment variables. In a few cases, quadratic or cubic functions were more appropriate for describing relationships. Following linear regression analysis, the resulting models were assessed for compliance with the assumptions of this analysis (residuals normally distributed with uniform variance along the regression line) and rejected where necessary. Relationships were considered significant when $p \leq 0.05$.

Analyses were conducted using Vespan, MINITAB 13.30 and SPSS 9.0.

2.4 Results

2.4.1 Summary statistics and species lists

During the vegetation surveys conducted between 2000 and 2002, 25 different aquatic plants were identified to species level at aquatic sub-sites. In addition, members of the Cyperaceae and Poaceae families and one member of the Lemnaceae family were recorded. A number of Onagraceae samples were identified as *Ludwigia* sp. but due to the absence of inflorescences at the sampling time, it was not possible to identify them to species level. *Chara* sp. was recorded twice and *Nitella* sp. once. The species list therefore includes aquatic plants belonging to 19 different families. *Mimosa* seedlings were occasionally recorded growing upon mats of *Salvinia* or in very shallow water. At one site, a terrestrial creeper, *Cayaponia podantha*, had reached from the bank where it was rooted and become intertwined with *Polygonum*. Table 2.3 shows the species list together with codes for the growth form of each species.

Table 2.3 Species recorded at aquatic sub-sites 2000-2002. Growth forms are indicated by letter codes: RF rooted-floating; FF free-floating; RE rooted-emergent; RS rooted-submerged; RE/S rooted with emergent and submerged leaves; T terrestrial.

Family	Identification	Authority	Growth form	Code
Apiaceae	<i>Hydrocotyle ranunculoides</i>	L.f.	RF	hyd
Araceae	<i>Pistia stratiotes</i>	L.	FF	pis
Cucurbitaceae	cf <i>Cayaponia podantha</i>	Cogn.	T	
Cyperaceae	Undetermined		RE	cyp
Fabaceae	<i>Mimosa pigra</i>	L.	T	mim
Haloragaceae	<i>Myriophyllum aquaticum</i>	(Vell.) Verdc.	E/RS	myr
Hydrocharitaceae	<i>Egeria densa</i>	Planch.	RS	ede
Hydrocharitaceae	<i>Egeria najas</i>	Planch.	RS	ena
Hydrocharitaceae	<i>Limnobium laevigatum</i>	(Humb. & Bonpl. ex Willd.) Heine	FF	lim
Lemnaceae	Undetermined		FF	lem
Lentibulariaceae	<i>Utricularia foliosa</i>	L.	S	utr
Najadaceae	<i>Najas</i> sp. (<i>microcarpa</i> ?)	(K. Schum.)	RS	naj
Nymphaeaceae	<i>Cabomba</i> sp. (<i>furcata</i> ?)	(Schult. & Schult. f.)	RS	cab
Nymphaeaceae	<i>Nymphaea amazonum</i>	Mart. & Zucc.	RF	nym
Onagraceae	<i>Ludwigia</i> sp.	L.	RE	lud
Poaceae	<i>Hymenachne amplexicaulis</i>	(Rudge.) Nees.	RE	gra
Poaceae	<i>Paspalum repens</i>	P.J. Berguis	RF	pas
Poaceae	Undetermined		RE	gra
Polygonaceae	<i>Polygonum acuminatum</i>	Kunth.	RE	pol
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.	RE	pfe
Polygonaceae	<i>Polygonum punctatum</i>	Elliott.	RE	pol
Polygonaceae	<i>Polygonum stelligerum</i>	Cham.	RE	pst
Pontederiaceae	<i>Eichhornia azurea</i>	Kunth.	RF	eaz
Pontederiaceae	<i>Eichhornia crassipes</i>	(Mart.) Solms	FF	ecr
Pontederiaceae	<i>Pontederia cordata</i>	L.	RE	pon
Potamogetonaceae	<i>Potamogeton pusillus</i>	L.	RS	ppu
Bryophyta:				
Ricciaceae	<i>Ricciocarpus natans</i>	(L.) Corda	FF	ric
Charophyta:				
Characeae	<i>Chara</i> sp.		RS	cha
Characeae	<i>Nitella</i> sp.		RS	nit
Pteridophyta:				
Azollaceae	<i>Azolla microphylla</i>	Kaulf.	FF	azo
Salvinaceae	<i>Salvinia auriculata</i>	Aubl.	FF	sal
Salvinaceae	<i>Salvinia herzogii</i>	de la Sota	FF	sal
Salvinaceae	<i>Salvinia minima</i>	Baker	FF	smi

Tables 2.4-2.12 show that a wide variation in each of the environmental, collective vegetation and dominant species trait variables was recorded in each year of sampling. Grazing intensity was the only exception as no evidence of grazing was observed at any of the aquatic sub-sites. The range observed in the environmental variables reflects the contrasting physical and chemical properties of the three different rivers which influence the study area, and also the variation within each river. These varying abiotic conditions in turn lead to the wide range observed in the collective vegetation and dominant species trait variables. Median values for each variable generally did not vary much between the three sampling years because a variety of waterbody types and locations were sampled in each year. The main differences between years were particularly high median water total Kjeldahl nitrogen in 2002 (associated with the relatively large number of temporary lagoon sites on the Paraná islands), and more reducing soil conditions in 2000 than in 2001 and 2002. In general, the measurements of environmental variables were reasonably similar to those reported by Murphy *et al.* (2003) from their survey conducted in 1999 and within the ranges recorded during several other studies in the floodplain waterbodies (Thomaz, Roberto & Bini 1997).

Table 2.4 Minimum, maximum and median or mode values of each environmental variable measured at 20 aquatic sub-sites in 2000.

Variable	Minimum	Maximum	Median	Mode
Water depth (m)	0.14	2.08	0.6	
Underwater light attenuation, k (m^{-1})	1.31	8.83	4.74	
Euphotic depth (m)	0.40	2.69	0.74	
Water pH	5.8	7.6	6.55	
Water conductivity ($\mu S cm^{-1}$)	25	158	44.5	
Water total Kjeldahl N ($\mu g L^{-1}$)	109.4	1112.4	352.0	
Water total P ($\mu g L^{-1}$)	4.86	85.76	17.02	
Sediment pH	4.9	7.0	6.4	
Sediment redox potential (mV)	-11	+720	382.5	
Sediment total Kjeldahl N ($mg kg^{-1}$)	180	6390	1440	
Sediment ADAS ext. P ($mg kg^{-1}$)	3.2	17.4	11.88	
Sediment total Fe ($mg kg^{-1}$)	15300	82500	31150	
Sediment total Ca ($mg kg^{-1}$)	215	10900	861	
Openness (1-5)	1	3		2
Grazing (1-5)	1	1		1
Shade (1-5)	1	3		1

Table 2.5 Minimum, maximum and median values of each collective vegetation variable measured at 20 aquatic sub-sites in 2000.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	2	11	6.6
Dry weight biomass (gm ⁻²)	141	2014	373
Canopy height (m)	0.03	2.47	0.8
Canopy cover (%)	15.44	100	64.2
Stem density (m ⁻²)	122	2156	400

Table 2.6 Minimum, maximum and median values of each dominant species trait variable measured at 20 aquatic sub-sites in 2000.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.01	51.26	10.69
Total root dry weight per plant (g)	0.01	13.00	2.06
Remainder dry weight per plant (g)	0.01	58.74	5.95
Total plant dry weight (g)	0.01	98.59	16.26
Maximum stem length (m)	0.04	1.69	0.74
Total leaf area per plant (cm ²)	10	4502	609
Specific leaf area (cm ² g ⁻¹)	55	1868	110

Table 2.7 Minimum, maximum and median or mode values of each environmental variable measured at 23 aquatic sub-sites in 2001.

Variable	Minimum	Maximum	Median	Mode
Water depth (m)	0.07	3.30	0.370	
Underwater light attenuation, k (m ⁻¹)	1.37	27.90	3.99	
Euphotic depth (m)	0.13	2.54	0.89	
Water pH	5.70	8.50	6.70	
Water conductivity (µScm ⁻¹)	14	110	30	
Water total Kjeldahl N (µg ⁻¹)	159.0	817.0	332.0	
Water total P (µg ⁻¹)	10.0	218.0	30.0	
Sediment pH	6.50	7.20	6.90	
Sediment redox potential (mV)	-166.0	277.0	-48.5	
Sediment total Kjeldahl N (mgkg ⁻¹)	52	13485	1097	
Sediment ADAS ext. P (mgkg ⁻¹)	0.45	54.21	14.03	
Sediment total Fe (mgkg ⁻¹)	3032	100000	36591	
Sediment total Ca (mgkg ⁻¹)	89	4861	808	
Openness (1-5)	1	3		2
Grazing (1-5)	1	1		1
Shade (1-5)	1	2		1

Table 2.8 Minimum, maximum and median values of each collective vegetation variable measured at 23 aquatic sub-sites in 2001.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	1	9	5.00
Dry weight biomass (gm^{-2})	1	3204	409
Canopy height (m)	0.06	3.59	0.52
Canopy cover (%)	18.33	100.00	62.22
Stem density (m^{-2})	100	3000	300

Table 2.9 Minimum, maximum and median values of dominant species trait variables measured at 23 aquatic sub-sites in 2001.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.13	58.88	4.50
Total root dry weight per plant (g)	0.01	32.35	2.41
Remainder dry weight per plant (g)	0.02	94.65	1.74
Total plant dry weight (g)	0.30	147.07	12.95
Maximum stem length (m)	0.04	2.02	0.75
Total leaf area per plant (cm^2)	31	4826	1199
Specific leaf area (cm^2g^{-1})	55	4505	138

Table 2.10 Minimum, maximum and median or mode values of environmental variables measured at 13 aquatic sub-sites in 2002.

Variable	Minimum	Maximum	Median	Mode
Water depth (m)	0.09	1.99	0.52	
Underwater light attenuation, k (m^{-1})	0.65	11.36	4.75	
Euphotic depth (m)	0.31	5.39	0.74	
Water pH	5.88	8.49	6.68	
Water conductivity (μScm^{-1})	18	54	32.00	
Water total Kjeldahl N (μgL^{-1})	320.40	1302.49	640.80	
Water total P (μgL^{-1})	14.42	71.93	27.28	
Sediment pH	6.19	7.46	6.94	
Sediment redox potential (mV)	-125	102	-41.5	
Sediment total Kjeldahl N (mgkg^{-1})	80	7890	2250	
Sediment ADAS ext.P (mgkg^{-1})	0.30	41.40	12.44	
Sediment total Fe (mgkg^{-1})	5210	73900	33000	
Sediment total Ca (mgkg^{-1})	76	2520	870	
Openness (1-5)	1	3		2
Grazing (1-5)	1	1		1
Shade (1-5)	1	3		1

Table 2.11 Minimum, maximum and median values of collective vegetation variables measured at 13 aquatic sub-sites in 2002.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	2	11	4
Dry weight biomass (gm ⁻²)	2	1535	477
Canopy height (m)	0.20	3.11	0.86
Canopy cover (%)	44.44	93.33	70.56
Stem density (m ⁻²)	36.1	733.3	108.3

Table 2.12 Minimum, maximum and median values of dominant species trait variables measured at 13 aquatic sub-sites in 2002.

Variable	Minimum	Maximum	Median
Total leaf dry weight (g)	0.46	99.47	14.07
Total root dry weight (g)	0.16	20.69	3.63
Remainder dry weight (g)	0	110.9	8.6
Total plant dry weight (g)	2.3	223.2	29.5
Maximum stem length (m)	0.14	2.33	1.39
Total leaf area per plant (cm ²)	85	13340	1674
Specific leaf area (cm ² g ⁻¹)	12.3	319.0	94.9

2.4.2 Identification of aquatic vegetation communities

TWINSPAN analysis of 2000 aquatic data

Three groups of sites were identified in the 2000 species data set using TWINSPAN analysis. At the first level of division, the site RPM was split off on its own because neither of its two species occurred at any other site (eigenvalue = 1). The division of the remaining nineteen sites was first into a group of seven, indicated by the presence of *Cyperus* sp., and a group of twelve composed of sites from which this species was absent (eigenvalue = 0.526). The group of twelve was then divided into a group of five indicated by the presence of *Nymphaea amazonum*, *Salvinia* sp. and *Egeria najas* and a second group of seven from which *Nymphaea* and *Egeria* were absent (eigenvalue = 0.398).

The relatively high eigenvalues indicate that the TWINSPAN divisions were based on substantial differences in the species composition of the three groups. However, because the data set is rather small in relation to the scale of the system being sampled, it does not make sense to continue dividing small groups as this would expand the data back to its

original unmanageable size. Interpretation of the TWINSpan analysis was therefore based on the three groups of sites differentiated on the basis of their species composition and abundance.

TWINSpan output

The TWINSpan output table orders sites and species so that sites with similar species assemblages are close together and species likely to occur in the same sites are close together. The diagonal pattern across the table represents species turnover across the sites listed from left to right. Some species occur only at the sites on the left (*Nymphaea*), some only in the sites in the middle (*Myriophyllum*), and some only in the sites on the right hand side (*Eichhornia crassipes*). *Eichhornia azurea*, on the other hand, occurs at almost all of the sites sampled (sixteen out of twenty) and so its presence does not easily contribute to the classification. Its frequency of occurrence suggests that it has a very wide ecological range and is able to grow with most of the floodplain species, although TWINSpan has separated its abundance scores, which are higher on the left hand side of the table than the right. It may respond to environmental variation by exhibiting differences in physical traits or abundance rather than presence and absence (see Section 2.4.6). *Paspalum repens* occurs in seven of the twenty sites but TWINSpan does not consider these sites similar according to their species composition. This grass therefore does not fit in well with the TWINSpan groups. Similarly, *Salvinia* sp. is placed at the extreme left and the extreme right of the table showing that these sites were not similar in other aspects. This could be the result of the group representing two species of *Salvinia*. There is a similar problem with the group *Polygonum* sp. which was not identified to species level at all sites. *Cabomba* and *Utricularia* are present at only very low frequency in the data set and at sites otherwise considered very different from each other (they are placed far apart in the table). They do not fit in very well with the classification. In addition, the data may not give a true representation of the distribution of submerged species such as *Utricularia*, *Cabomba*, *Myriophyllum* and *Najas* because these species are inconspicuous during sampling and so are less likely to be recorded than other species.

Comparisons of TWINSpan groups

Site locations and species compositions

Group I represents sites with a mixed community of several species, each of which occurred at moderate to high abundance. *Eichhornia azurea* was present at almost all sites but was not dominant at any of them. Instead, the community consisted mainly of free-

floating species, including *E. crassipes*, *Limnobium laevigatum* and *Hydrocotyle ramunculoides*, which did not occur in either of the other groups. The most frequent dominant was *Salvinia* sp. which had the greatest abundance at all but one site. In this community, *E. azurea* may be providing refuges between its stems for the floating species, protecting them from flow disturbance. Most of the sites in group I were associated with various waterbody types of the Baía River (three main channel sites, one open lagoon site and one site on the Curutuba channel which links the Baía and Ivinheima Rivers).

Group II sites comprised a variety of locations and waterbody types across both the Baía River and the Paraná River. *E. azurea* dominated the vegetation at all but one site where *Paspalum repens*, which has a similar floating stem morphology, dominated instead. Most other species were in low abundance. None of the species recorded was unique to this group.

Group III sites supported *Nymphaea amazonum* and *Egeria najas* which were absent from all other sites. Three different species dominated across the sites, with *E. azurea* at only one site. All of the sites in this group were associated with the Paraná River.

Table 2.13 summarises the main environmental, vegetation and dominant species trait characteristics of the three TWINSpan groups. Mean or median values of each variable are given in Tables 2.14 and 2.15, together with p-values indicating the significance of differences between groups.

Table 2.13 Summary of 2000 TWINSpan group characteristics.

TWINSpan Group	I	II	III
Number of sites	7	7	5
Indicator species	Presence of <i>Cyperus</i> sp.	None	Presence of <i>Nymphaea amazonum</i> , <i>Salvinia</i> sp., <i>Egeria najas</i> .
Predominant river association	Baía	Baía-Paraná mixed	Paraná
Environmental characteristics	Deep water, euphotic zone does not extend to bottom.	Shallow water, intermediate light penetration to sediment.	Shallow water, good light supply to sediment.
Vegetation characteristics	Tall, species-rich vegetation with high cover and stem density.	Shorter vegetation with fewer species. Low cover and stem density.	Shorter vegetation with fewer species. High cover, intermediate stem density.
Traits of dominant species	Short stems with intermediate root weight.	Long stems with high root weight.	Intermediate stem length with low root weight.

Environmental comparisons

Group I sites were characterised by deep water (significantly deeper than at the sites in groups II and III). In most cases, the euphotic zone did not extend to the bottom, preventing the growth of small, rooted, submerged plants (Zeu/d significantly less than in group II) (Table 2.14).

Group II and III sites had shallow water that permitted sufficient light for photosynthesis to reach the bottom allowing the growth of submerged, rooted species.

No other environmental variables differed significantly between groups (Table 2.14).

Table 2.14 Means, standard errors (S.e.) and significance of differences (one-way ANOVA) between TWINSpan groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate that Tukey's multiple comparisons showed they were significantly different. *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Water depth (m)	1.29 ^a	0.23	0.51 ^b	0.11	0.51 ^b	0.17	0.008
Underwater light attenuation, k (m ⁻¹)	4.32	0.69	5.79	0.83	3.08	1.44	0.193
Euphotic depth/water depth	0.91 ^a	0.20	1.74 ^{ab}	0.60	4.62 ^b	1.56	0.008
*Water conductivity (µS cm ⁻¹)	48		44		45		0.995
Water pH	6.54	0.23	6.53	0.20	6.78	0.13	0.648
Water total P (µg L ⁻¹)	18.95	4.54	41.3	13.0	13.19	5.46	0.111
Water total Kjeldahl N (µg L ⁻¹)	376.3	59.7	436	118	353.7	50.8	0.931
Sediment redox potential (mV)	394.7	85.4	378	79.8	272.4	83.9	0.589
Sediment pH	5.97	0.30	6.46	0.19	6.44	0.38	0.390
Sediment ADAS ext. P (mg kg ⁻¹)	9.21	1.71	10.63	1.24	10.12	2.45	0.832
Sediment total Kjeldahl N (mg kg ⁻¹)	1334	366	2720	742	1740	534	0.176
Sediment total Fe (mg kg ⁻¹)	41014	9263	30500	3347	45920	7349	0.329
Sediment total Ca (mg kg ⁻¹)	827	221	2839	1384	847.6	93.1	0.090

Table 2.15 Means, standard errors (S.e.) and significance of differences (one-way ANOVA) between TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate that Tukey's multiple comparisons showed they were significantly different. *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	9.43 ^a	0.78	5.00 ^b	0.82	5.60 ^b	0.51	0.001
*Dry weight biomass (gm ⁻²)	1109.9		403.9		345.6		0.250
Canopy height (m)	1.55 ^a	0.25	0.75 ^b	0.09	0.70 ^b	0.19	0.009
Canopy cover (%)	83.87 ^a	7.72	32.40 ^b	6.03	76.67 ^a	6.41	<0.001
Stem density (m ⁻²)	743 ^a	249	238.1 ^b	50.7	511 ^{ab}	156	0.044
Total leaf dry weight per plant (g)	7.27	4.44	15.01	4.67	11.58	9.96	0.270
Total leaf area per plant (cm ²)	612	216	1043	234	1248	824	0.482
*Specific leaf area (cm ² g ⁻¹)	186.91		77.11		215.83		0.196
Total root dry weight per plant (g)	3.05 ^{ab}	1.64	6.76 ^a	1.59	1.23 ^b	0.86	0.031
Remainder dry weight per plant (g)	10.00	8.23	18.81	3.46	13.91	8.77	0.220
Total plant dry weight (g)	20.3	13.3	40.57	8.06	26.70	18.9	0.233
Leaf weight / root weight ratio	4.02	1.24	3.41	1.96	12.93	4.91	0.156
Maximum stem length (m)	0.39 ^a	0.16	1.33 ^b	0.10	0.79 ^{ab}	0.28	0.004

Collective vegetation comparisons

Group I vegetation was significantly taller and more species rich than vegetation in groups II or III. Percentage canopy cover was significantly greater than in group II but similar to group III. Stem density was significantly greater in group I than II and intermediate in group III (Table 2.15).

Group I vegetation was therefore tallest and most species rich with high canopy cover and stem density. Group II vegetation was short with lowest canopy cover and stem density and low species richness. Group III vegetation was also short with high canopy cover, intermediate stem density and low species richness.

Comparisons of traits of dominant species

In measurements of dominant species traits, only maximum stem length and total root weight differed significantly between groups. Group II dominants had significantly longer stems than group I and significantly greater root weight than group III (Table 2.15). The long stems and heavy roots of group II reflect the strong dominance of the bulky species *Eichhornia azurea* at all but one site. The short stems of group I dominants are due to the

importance of small ferns, *Salvinia* sp., in this group. The low root weight in group III is linked with the generally small and lightweight structure of submerged, rooted species which featured in this mixed group of life-forms which also included free-floating, rooted-floating and emergent species.

RPM characteristics

The remaining site, RPM, differed in many ways from the TWINSpan groups. Water phosphorus and sediment phosphorus were lower at this site than at any other. Sediment nitrogen and calcium were particularly low in relation to other sites, and the most reducing redox conditions were recorded here. Vegetation height, biomass and species richness were also at their lowest. These differences can be explained by the location of this site in the main channel of the Paraná where no other sites were sampled. Studies by Thomaz, Roberto & Bini (1997) have shown that the main channel has the greatest water velocity, clarity, pH, conductivity and alkalinity and the lowest water nitrogen and phosphorus levels found in the floodplain. The fast-flowing, clear water is therefore very suitable for the growth of the small, streamlined, submerged species found there, for example, *Potamogeton pusillus*.

TWINSpan analysis of 2001 aquatic data

TWINSpan analysis of the species data collected in 2001 divided the sites into four groups, each representing a vegetation type. At the first division, sites colonised exclusively by rooted, submerged plants were separated from the remaining sites with an eigenvalue of 1, indicating that the two groups had no species in common. The indicator species for this group, group I, were *Potamogeton pusillus* and *Egeria najas*. Group II was split off from the remaining nineteen sites with an eigenvalue of 0.494, indicating that although some species occurred in both groups, the overall pattern of distribution and abundance of species was very different between them. This group was indicated by a moderate abundance of *Eichhornia crassipes* and *Nymphaea amazonum*. At the third level of division, the last fourteen sites were separated into a group of five, group III, indicated by a moderate abundance of *Salvinia minima*, and a group of nine, group IV (eigenvalue = 0.440, again indicating that the two resulting groups were substantially different).

Comparisons of 2001 TWINSPAN groups

Site locations and species compositions

Group I consisted of sites closely associated with the main channel of the Paraná River (two main channel sites, one backwater site and one site located on the Cortado channel which is connected at both ends to the main Paraná channel) supporting four rooted, submerged species with adaptations suiting them to fast-flowing, clear water. Their flexible, streamlined structure prevents potential damage by water movement in the faster-flowing channels. In addition, fast-flowing water can enhance photosynthesis in submerged species by reducing the static boundary layer surrounding the leaf surface and facilitating gas exchange (Wetzel 1983). As could be expected, the main channel Paraná sites were similar in vegetation and environmental characteristics to RPM sampled in the main channel in 2000. However, although potentially strongly influenced by the main Paraná channel due to their proximity to it, the backwater and Cortado channel sites had slower water flow conditions.

Sites in group II were dominated by *Eichhornia crassipes*, *E. azurea* or *Nymphaea amazonum*. *E. azurea* occurred at only one site differentiating this group from groups III and IV in which *E. azurea* was recorded at every site. Four of the five sites in this group were associated with the Baía River.

Group III was a mixed group of free-floating species with a moderate abundance of *E. azurea* at every site. This suggests a comparison with 2000 group I which shared these characteristics. *E. azurea* again may have been playing a sheltering role, encouraging colonisation of the water surface exposed between its stems. The sites in this group were associated with semi-lotic to lotic habitats in the Baía and Ivinheima Rivers, as well as Curutuba channel which connects them.

E. azurea was an important component of group IV and was the dominant species at six of the nine sites. This appeared to limit the success of additional species which were few in number and occurred at moderate to low abundance. Sites in group IV were located on the Baía, Ivinheima and Paraná Rivers but were mainly associated with semi-lotic habitats.

The principal environmental, vegetation and dominant trait characteristics of the 2001 TWINSPAN groups are summarised in Table 2.16. Mean values of each variable are given in Tables 2.17 and 2.18, together with p-values indicating the significance of differences between groups.

Table 2.16 Summary of 2001 TWINSPAN group characteristics.

TWINSpan Group	I	II	III	IV
Number of sites	4	5	5	9
Indicator species	<i>Potamogeton pusillus</i> , <i>Egeria najas</i> .	Moderately abundant <i>Eichhornia crassipes</i> & <i>Nymphaea amazonum</i> .	Moderately abundant <i>Salvinia minima</i> .	
Predominant habitat type	Paraná main channel.	Baía semi-lotic to lentic.	Baía-Ivinheima semi-lotic to lotic.	All rivers, semi-lotic.
Environmental characteristics	High water conductivity. Slightly alkaline water pH.	Intermediate pH and conductivity.	Low water conductivity. Slightly acidic water pH.	Intermediate conductivity. Slightly acidic water pH.
Vegetation characteristics	Short, high stem density, intermediate species richness.	Low stem density, intermediate vegetation height & species richness.	Tall, high species richness, intermediate stem density.	Intermediate height, low stem density & species richness.
Traits of dominant species	Lightweight plants, low root investment.	Heavy, thick leaves, high total weight, light stems.	Intermediate between other groups.	Heavy leaves, stems and total weight.

Environmental comparisons

A number of environmental factors were recorded at each site but only water pH and conductivity were found to differ significantly ($p \leq 0.05$) between TWINSPAN groups (Table 2.17). Water was most alkaline and of highest conductivity at group I sites located in the Paraná, which tends to carry greater concentrations of inorganic salts than the other rivers (Thomaz, Roberto & Bini, 1997). pH was significantly lower in groups III and IV than group I. Conductivity was similar in groups II and IV to all other groups but significantly lower in group III than group I. Sediment phosphorus and nitrogen may also be important in controlling the vegetation communities recorded. Although the values were not considered significantly different between groups, p was close to 0.05. Mean sediment phosphorus was greatest in group IV, slightly lower in group III and lower still in group II. It was much lower in group I ($p = 0.064$). Sediment nitrogen followed a similar pattern. It was greatest in group IV then lower in group III and lower still in group II. It was a lot lower in group I ($p = 0.063$). Particularly low nutrients are expected in main channel Paraná sites such as those in group IV (Thomaz, Roberto & Bini 1997).

Table 2.17 Means, standard errors (S.e.) and significance of differences (one-way ANOVA) between 2001 TWINSpan groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate that Tukey's multiple comparisons showed they were significantly different. *Medians are quoted for non-normal variables compared using Kruskal-Wallis tests.

Variable	Group I		Group II		Group III		Group IV		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Water depth (m)	0.44	0.33	0.83	0.31	1.11	0.56	0.58	0.20	0.233
Underwater light attenuation, k (m^{-1})	3.51	0.76	4.88	0.75	4.17	0.81	8.22	2.8	0.566
Z_{ov}/d	10.16	3.44	1.57	0.53	2.04	0.92	2.24	0.54	0.212
Water pH	7.47 ^a	0.38	6.62 ^{ab}	0.24	6.54 ^b	0.18	6.61 ^b	0.10	0.035
Water conductivity ($\mu S cm^{-1}$)	64.2 ^a	15.3	33.40 ^{ab}	7.19	20.90 ^b	2.28	42.00 ^{ab}	7.88	0.027
Water total P ($\mu g L^{-1}$)	24.75	7.19	61.0	31.7	69.2	32.9	58.9	22.4	0.666
Water total Kjeldahl N ($\mu g L^{-1}$)	393	129	472	73.3	464	113	386	77.8	0.793
*Sediment redox potential (mV)	-114.50		-3.05		6.00		-99.00		0.810
Sediment pH	6.95	0.15	6.78	0.10	6.84	0.12	6.91	0.05	0.619
Sediment ADAS ext. P ($mg kg^{-1}$)	5.24	1.72	16.31	4.20	20.83	7.91	24.34	5.48	0.064
Sediment total Kjeldahl N ($mg kg^{-1}$)	787	543	2355	1789	3596	2496	4152	1183	0.063
Sediment total Fe ($mg kg^{-1}$)	26485	13364	29712	7613	42724	17317	64404	9730	0.106
Sediment total Ca ($mg kg^{-1}$)	1497	1132	1118	661	1947	919	1960	338	0.314

Collective vegetation comparisons

The TWINSpan groups showed greater contrasts in collective vegetation structure (Table 2.18). Vegetation height was significantly greater in group III than group I and species richness significantly greater in group IV than group III. Stem density was significantly greater in group I than in group II or IV. Group IV had the lowest stem density, significantly lower than in group II. Biomass did not differ significantly between groups.

Table 2.18 Mean, standard error (S.e.) and significance of differences (one-way ANOVA) between 2001 TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate that Tukey's multiple comparisons showed they were significantly different. *Medians are quoted for non-normal variables compared using Kruskal-Wallis tests.

Variable	Group I		Group II		Group III		Group IV		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	2.75 ^{ab}	1.18	4.60 ^{ab}	1.03	6.40 ^a	0.75	3.33 ^b	0.55	0.033
*Dry weight biomass (gm ⁻²)	122		935		490		615		0.088
Canopy height (m)	0.08 ^a	0.01	0.92 ^{ab}	0.36	1.35 ^b	0.57	0.78 ^{ab}	0.20	0.018
Canopy cover (%)	83.70	13.1	60.22	13.4	74.55	6.87	54.63	8.41	0.261
Stem density (m ⁻²)	1774 ^a	616	300 ^{bc}	157	638 ^{ab}	183	211 ^c	27	<0.001
Total leaf dry weight per plant (g)	0.51 ^a	0.13	20.0 ^b	10.3	12.7 ^{ab}	11.9	17.09 ^b	5.77	0.020
Total leaf area per plant (cm ²)	985	292	1374	556	1382	1151	1528	409	0.871
*Specific leaf area (cm ² g ⁻¹)	2486 ^a		119 ^b		217 ^{ab}		135 ^{ab}		0.018
Total root dry weight per plant (g)	0.02	0.01	14.17	6.01	8.37	8.14	6.48	2.26	0.082
Remainder dry weight per plant (g)	0.005 ^a	0.005	2.35 ^{ab}	1.39	13.5 ^{ab}	11.6	26.5 ^b	10.2	0.044
Total plant dry weight (g)	0.53 ^a	0.13	36.5 ^b	13.5	30.4 ^{ab}	27.6	49.3 ^b	16.0	0.002
Leaf weight/ root weight	24.33 ^a	8.19	1.85 ^b	0.66	1.75 ^b	1.18	2.81 ^b	1.01	0.007
Maximum stem length (m)	21.50	6.66	54.8	19.2	109.6	41.1	111.2	24.1	0.104

Group I vegetation had the lowest canopy height resulting from the exclusively submerged life-forms in this group. In the other groups with floating vegetation, the height above the sediment was largely related to water depth. The small size and vertical-growing structure of the submerged plants also gave group I the highest stem density. Species richness was intermediate. Group II vegetation had a low stem density and was intermediate in vegetation height and species richness. The predominance of *Eichhornia crassipes* with its rosette life-form results in individuals being spaced out by the leaves radiating from each central point (which was counted as the stem). Group III vegetation was tallest (this group had the greatest mean water depth) and most species rich with intermediate stem density.

Group IV vegetation had low stem density and species richness and was of intermediate height. The large size of the very frequent *E. azurea* prevented a high stem density but still allowed it to cover large areas of water close to the bank in which it was rooted. Its strong dominance in this group is also likely to prevent other species from becoming successful.

Comparisons of traits of dominant species

Total leaf weight per plant was significantly lower in group I than in groups II or IV which had similar leaf weights. Remainder weight (in most cases equivalent to stem weight, although any inflorescences were included) was significantly greater in group IV than in group I while it was intermediate in groups II and III. Total plant dry weight was significantly lower in group I than in groups II or IV and intermediate in group III. The ratio of leaf weight to root weight was significantly greater in group I than in any of the other groups. The thinnest leaves were in group I where specific leaf area was significantly greater than in group II.

Group I was represented by small, lightweight dominant species. The investment in leaf weight in relation to root weight was greater than in other groups. However, this result may be distorted by the difficulty in removing all of the roots from the sediment. This morphology is consistent with the expected adaptations to fast-flowing, clear water such as is found in the main channel of the Paraná.

Group II dominants had heavy, thick leaves contrasting with group I. *E. crassipes* dominated at three of the five sites with the bulky species *E. azurea* and *N. amazonum* at the remaining sites.

Group III sites were dominated by species with contrasting morphologies and life-forms. These were stoloniferous, rooted-floating *Hydrocotyle ramunculoides*, rosette forming, free floating *E. crassipes*, two species of free-floating ferns, and bulky *E. azurea*. This resulted in mean values for traits which were intermediate between those recorded in other groups, or similar.

Like group II, group IV dominants had heavy leaves, stems and total dry weights per plant. In this group, *E. azurea* was dominant at most sites contributing a greater stem weight than *E. crassipes* did in group II.

TWINSPAN analysis of 2000-2001 data set

TWINSPAN analysis of species data collected from 43 aquatic sites during spring 2000 and 2001 resulted in three major groups of sites representing separate vegetation types. Table 2.19 summarises the main characteristics of these groups. In the first division, RPM was split off from the other sites due to the unique occurrence of *Nitella* at this site. However, RPM corresponded well with vegetation group III, which was split off at the second level of division with a high eigenvalue (0.764), as it had in common with these sites a species assemblage consisting exclusively of submerged, rooted life-forms. This group was indicated by the presence of *Potamogeton pusillus*, and by abundant *Egeria najas*. Although frequently dominant elsewhere, *Eichhornia azurea* and *Eichhornia crassipes* were absent from this group.

The remaining 38 sites were divided into groups I and II, each with 19 sites, with an eigenvalue of 0.449 indicating that they were substantially different in species assemblage.

Table 2.19 Summary of 2000-2001 TWINSPAN group characteristics.

TWINSPAN Group	I	II	III
Number of sites	19	19	5
Indicator species	Presence of <i>E. crassipes</i> , <i>Limnobium laevigatum</i> , <i>Cyperus</i> sp., abundant <i>Salvinia</i> spp.	Abundant <i>E. azurea</i> , presence of <i>Nymphaea amazonum</i> .	Presence of <i>Potamogeton pusillus</i> , abundant <i>Egeria najas</i> .
Predominant habitat type	Semi-lotic to lotic habitats associated with Baía and Ivinheima.	Lentic to semi-lotic habitats associated with Paraná.	Lotic, main Paraná channel.
Environmental characteristics	Deep, acidic-neutral, low conductivity water. Little light at bottom. Sediment rich in N and P.	Shallow, acidic-neutral high conductivity water. Moderate light at sediment. Sediment rich in N and P.	Shallow, alkaline-neutral, intermediate conductivity water. Good light availability at bottom. Sediment poor in N and P.
Vegetation characteristics	High biomass, height, cover, species richness, low stem density.	Intermediate biomass, height, species richness, low cover, stem density.	Low biomass, height, species richness, high stem density, intermediate cover.
Traits of dominant species	Intermediate leaf, root, remainder & total weight & thickness, small leaf area.	Large, heavy, thick leaves, long, heavy stems, intermediate root weight.	Small leaf area, weight, thickness, low root, remainder, total weight.

Comparisons of 2000-2001 TWINSPAN groups

Site locations and species compositions

Group I was indicated by *E. crassipes* which shared dominance with a variety of other species. This was a species-rich group consisting mainly of floating and emergent species in high abundance including *Salvinia* sp., *Salvinia minima*, *Cyperus* sp. (which often rooted within floating mats of *Salvinia*), *Hydrocotyle ramunculoides*, *Limnobium laevigatum* and *Polygonum ferrugineum* in addition to frequent *E. azurea*.

Group I consisted mainly of sites on the Baía and Ivinheima Rivers, including three sites on Canal Curutuba which links the two rivers. Eleven of the sixteen sites sampled on the Baía, and six of the seven sites sampled on the Ivinheima, were included in this group. The diversity of species and life-forms seen in group I sites could be due to the varied habitats within the Baía and Ivinheima which, at least during the dry season, may be influenced by more local processes than by the larger-scale processes which affect the Paraná. The Baía River, for example, widens out upstream from its connection with the Paraná and forms a patchwork of semi-lotic, open lagoons, permanent, closed lagoons and a fast-flowing main channel with undefined banks that merges into wetland vegetation. This provides a variety of habitat types to suit the range of species found in these sites.

Sites in group II were mostly strongly dominated by high abundances of *E. azurea*, which was an indicator species, with a limited number of other species present, each at rather low frequency relative to group I. *Nymphaea amazonum* occurred exclusively within group II and was also an indicator species, while *E. crassipes* was very rare.

Group II consisted mainly of sites associated with the Paraná including open lagoons and backwaters, closed, temporary lagoons located on islands within the river channel, and a few sites in the Baía close to where it meets the Paraná. These waterbodies can therefore make exchanges with the Paraná, some all year round, except when the water level is at its very lowest, and others only when the river overtops the banks of the islands during floods. Group II sites had lower species richness and evenness than group I sites. The extreme dominance of *E. azurea* suggests that these are the most suitable habitats for its growth.

Group III was characterised by submerged species and consisted of five sites closely associated with the Paraná channel. In 2000, the only site supporting a purely submerged community was located in clear, fast-flowing water at the edge of the main Paraná channel, and in 2001, two more main channel sites were found to support submerged species

exclusively. This association suggested that the habitat type was particularly suitable for streamlined, flexible submerged species but not floating or emergent species, which could be washed away or damaged by the high water velocity. The fast current could be expected to facilitate gas exchange by the submerged macrophytes by minimising the boundary layer surrounding leaf surfaces while the clear water would maximise light availability. However, in 2001, one of the sites was in a lotic backwater (disconnected from the main channel at the time of sampling due to a particularly low river level) and a second was a semi-lotic channel connected at both ends to the main Paraná channel. Flow in these habitats was slower than in the main channel habitats, indicating that the submerged species were not dependent upon fast-flowing water. Thomaz *et al.* (2004) noted that the occurrence of submerged species has been increasing in recent years in lagoons and backwaters connected to the Paraná River and in slower-flowing areas of the main channels of the Baía and Paraná Rivers. They comment that this change has coincided with increasing water clarity since Porto Primavera Reservoir was established and with increasing inputs of the propagules of submerged species from the chain of reservoirs upstream where some species have become abundant.

Subsequent divisions of groups I and II appeared to be based upon the presence or absence of species which were relatively rare in the floodplain, increasing the likelihood that their recorded distribution was due to chance. The data set therefore shows three distinct vegetation types, the differentiation of which must be controlled by the combination of biotic and abiotic factors operating at different locations within the floodplain. In order to investigate the factors responsible for determining the vegetation types, environmental, vegetation and dominant plant trait characteristics were compared between the groups of sites. Mean values of each variable together with the significance of any differences between groups are given in Tables 2.20 and 2.21.

Table 2.20 Means, standard errors (S.e.) and significance of differences (one-way ANOVA) between 2000-2001 TWINSPAN groups of normally distributed variables (data back-transformed as necessary). Contrasting superscript letters between groups indicate that Tukey's multiple comparisons showed them to be significantly different.

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Water depth (m)	1.11 ^a	0.19	0.37 ^b	0.07	0.43 ^b	0.26	0.002
k (m ⁻¹)	5.20	0.53	5.66	1.45	3.23	0.65	0.364
Euphotic depth / water depth	1.27 ^a	0.28	2.98 ^b	0.56	8.96 ^b	2.92	<0.001
Water pH	6.55 ^a	0.11	6.64 ^a	0.08	7.47 ^b	0.29	0.002
Water conductivity (μScm ⁻¹)	35.61 ^a	5.72	51.89 ^b	7.05	60.0 ^{ab}	12.6	0.018
Water total P (μg L ⁻¹)	40.16	9.85	47.7	14.1	29.9	8.82	0.925
Water total Kjeldahl N (μg L ⁻¹)	408.9	47.3	412.8	50.8	369	103	0.895
Sediment ADAS ext. P (mg kg ⁻¹)	18.04 ^a	3.51	16.93 ^a	2.16	4.74 ^b	1.43	0.016
Sediment total Kjeldahl N (mg kg ⁻¹)	2650 ^a	853	2834 ^a	582	676 ^b	435	0.004
Sediment total Fe	39213	6662	48788	5190	26268	10354	0.093
Sediment total Ca	1308	311	2001	540	1267	907	0.068
Number of species (per sub-site)	6.95 ^a	0.61	4.316 ^b	0.48	2.6 ^b	0.93	<0.001
Canopy cover (%)	76.86 ^a	4.82	47.49 ^b	5.46	70.8 ^{ab}	15.9	0.001
Stem density (m ⁻²)	557 ^a	111	285.2 ^b	56.9	1467 ^c	533	<0.001
Maximum stem length (m)	0.66 ^a	0.14	1.18 ^b	0.12	0.19 ^a	0.06	<0.001

Environmental comparisons

Group I sites were characterised by deep water (significantly deeper than group II but not group III) which was significantly lower in conductivity and had more acidic pH than group II (but similar in both cases to group III). In general, there was insufficient light reaching the sediment for photosynthesis to take place throughout the water column (significantly lower than groups II and III). Sediment nitrogen and phosphorus levels were significantly higher than in group III but similar to group II.

Group II sites had the shallowest water, acidic-neutral pH, high conductivity (significantly higher than group I), nitrogen and phosphorus-rich sediments and a moderately good light supply for photosynthesis at the sediment surface.

Group III sites were similarly shallow, had significantly more alkaline water pH than the other groups, moderate conductivity and the greatest light availability at the sediments. Nitrogen and phosphorus levels in the sediment were significantly lower than in other groups.

The light extinction coefficient, openness, shade, total water nitrogen and phosphorus; and sediment redox potential, pH, iron and calcium content did not differ significantly between groups.

Table 2.21 Median values and significance of differences between 2000-2001 TWINSpan groups (Kruskal-Wallis tests) of variables which were not normally distributed. Contrasting superscript letters indicate that an appropriate multiple comparison test (Siegel and Castellan 1988, pp. 213-214) showed they were significantly different.

Variable	Group I	Group II	Group III	p
Sediment redox potential	53.4	167	-83	0.145
Sediment pH	6.7	6.9	7.0	0.093
Vegetation height (m)	1.08 ^a	0.52 ^b	0.06 ^c	<0.001
Dry weight biomass (gm ⁻²)	962 ^a	345.5 ^b	140.5 ^b	<0.001
Total leaf dry weight per plant (g)	3.93 ^{ab}	9.03 ^a	0.37 ^b	0.019
Total leaf area per plant (cm ²)	500	1014	1182	0.467
Specific leaf area (cm ² g ⁻¹)	149.2 ^{ab}	103.5 ^a	1374.7 ^b	0.007
Total root dry weight per plant (g)	3.40 ^a	2.75 ^a	0.01 ^b	0.004
Remainder dry weight per plant (g)	0.67 ^a	20.37 ^b	0.01 ^{ac}	<0.001
Total plant dry weight (g)	12.12 ^a	38.29 ^a	0.38 ^b	0.005

Collective vegetation comparisons

The groups also differed in collective vegetation characteristics (measured regardless of species). Stem density was lowest in group I, intermediate in group II and greatest in group III. All of these differences were significant. Similarly, vegetation height differed significantly between all three groups and was greatest in group I, intermediate in group II and lowest in group III. At sites where floating vegetation was present, vegetation height was strongly influenced by water depth because the measurement was made from the sediment surface to the top of the tallest shoot. The average number of species per sub-site was significantly greater at group I sites and similar between group II and III sites. Biomass and stem density were significantly greater in group I sites than in groups II and III in which they were similar.

Group I was therefore the most species rich, with tall, high biomass vegetation with a high percentage canopy cover but low stem density. Group II had low canopy cover, intermediate vegetation height, stem density, biomass and species richness. Group III had the highest stem density but the lowest vegetation height, biomass and species richness. Canopy cover was intermediate.

Comparisons of traits of dominant species

Comparison of morphological traits of the dominant species at each site in each group showed that the groups differed in their average values.

Group II was represented by large, thick, heavy leaves (significantly heavier and thicker than in group III), long, heavy stems (significantly longer stem than in group I and greater remainder weight than in groups I and III), intermediate root weight and high total weight (both significantly greater than group III). These results reflect the dominance of *E. azurea* at most of the sites in this group. This is a large species with long stems that stretch from the bank, where they are rooted, out across the water surface. Both leaves and roots occur along the length of the stem. Root investment was not great in this group (high leaf weight : root weight ratio) possibly because access to the sediments provided a greater supply of nutrients than the water itself.

In contrast, group III was represented by the smallest leaf area, shortest stem length (significantly shorter than group II), lightest, thinnest leaves (both significantly different from group II), and lowest total plant weight (significantly different from groups I and II). This was due to the submerged form of the species occurring at sites in this group. They must have a feathery and flexible form to avoid damage by fast-flowing water and therefore are small and lightweight. The fragile nature of these species made efficient collection of roots rather difficult and so, although they appeared to be fairly small and lightweight, the whole root system was probably not collected and weighed.

Group I showed average trait values intermediate between these two extremes. This is due to the mixture of dominant species found in this group, and because of the frequent floating rosette life-form which is larger than the submerged plants, but smaller than those with long stolons such as *E. azurea* and *Paspalum repens*. There was greatest investment in roots in this group (low leaf weight : root weight ratio) possibly to aid uptake of nutrients directly from the water in the surface-floating species.

Comparison of 2000-2001 vegetation communities with 1999 results

By studying the outcomes of the analysis of both the 2000-2001 vegetation and environment data and the results of analysis of similar aquatic surveys conducted in 1999 (Table 2.22) (Murphy *et al.* 2003), a more detailed picture of the vegetation types of the Paraná floodplain can be deduced.

The most obvious difference between the two sets of results is the presence of an entirely submerged community in 2000-2001. This was not recorded in 1999, probably because no sites were located within the main channel of the Paraná. Alternatively, this may reflect a recent increase in submerged species in the floodplain, possibly due to increased water transparency and propagule inputs from upstream sources (Thomaz *et al.* 2004). There are therefore two remaining 2000-2001 groups that can be compared with the three vegetation types found in 1999. Studying the TWINSpan output tables suggests that 1999 groups B and C may be sub-groups of 2000-2001 group II. Alternatively, 1999 group C may represent a rarer community type which was not encountered sufficiently often in 2000 or 2001 to produce a separate grouping. 2000-2001 group I seems to correspond with 1999 group A.

Table 2.22 Summary of 1999 TWINSpan group characteristics.

TWINSpan Group	A	B	C
Number of sites	9	30	6
Indicator species	Moderately abundant <i>Cyperus diffusis</i> , presence of <i>Limnobium laevigatum</i> .	Absence of <i>Limnobium laevigatum</i> .	Absence of <i>Salvinia</i> spp.
Predominant habitat type	Semi-lotic to lotic.	Mixed; mainly slow-flowing.	Semi-lotic to lentic.
Environmental characteristics	Water deep & clear; low conductivity, alkalinity & P. Low sediment Fe, Ca & P; high N.	Intermediate depth, less clear water. Intermediate water pH, conductivity, P; high alkalinity. Intermediate sediment Ca & Fe; high N & P.	Shallow, less clear water. High water P & conductivity. High sediment Ca & Fe, intermediate P, low N.
Vegetation characteristics	Dominated by <i>E. azurea</i> ; abundant free-floating species. High biomass and species diversity.	Dominated by <i>E. azurea</i> ; abundant free-floating or emergent species. High biomass, intermediate species diversity.	<i>Nymphaea amazonum</i> moderately abundant, submerged species. <i>E. azurea</i> less common. Low species diversity.
Traits of dominant species	Small, lightweight plants.	Large, heavy plants.	Intermediate size dominants.

In both 1999 group A and 2000-2001 group I, *E. azurea* was very common, but free-floating species were also abundant. The water at these sites was deep and of low conductivity while sediments were nitrogen-rich. Biomass and species richness were high in relation to the other groups from the same years. The dominant species were relatively small and light.

2000-2001 group II appeared to incorporate features of 1999 groups B and C. In 2000-2001 group II, *E. azurea* was strongly dominant as in 1999 group B. However, group II also included sites that supported *N. amazonum* which in the 1999 groups occurred only in group C. 1999 groups B and C also had environmental conditions in common with 2000-2001 group II. Water at these sites was relatively slow flowing and shallow with high conductivity and the sediment was rich in nitrogen and phosphorus. In both data sets, biomass and species richness were intermediate for this type of vegetation. The dominant species tended to be large and heavy.

2.4.3 Ordination analysis: uncovering vegetation and environmental gradients in the species data

DCA analysis of aquatic species data

2000 DCA

DCA ordination of all sites sampled in 2000 produced a site ordination diagram with RPM at the far right hand side of axis one and all of the other sites confined to axis two. RPM was an unusual site because there were only two species growing there, neither of which was recorded at any other site. The contrast in species composition at RPM is easily understood because this was the only sampling site located in the main channel of the Paraná River where physical and chemical conditions are markedly different from the other areas studied. DCA focused on this feature of the data, disguising relationships between the remaining nineteen sites, and so RPM was deleted from subsequent analyses.

Figure 2.7 is a DCA site ordination diagram of the aquatic plant survey data collected in 2000 (RPM deleted from analysis). The diagram illustrates the relationships between the sites with respect to the species recorded at them. It is likely that sites located close together in the diagram supported similar species assemblages, while those that are far apart had few species in common. The two axes represent gradients of species turnover so that plant communities at sites with points located at the left hand side of the diagram were probably very different from those with points at the right hand side. A gradient length on axis one of four standard deviations (s.d.) tends to indicate complete species turnover in the diagram so that the point furthest to the left shares no species with the point furthest to the right (Jongman, ter Braak & van Tongeren 1995, p. 107). In this ordination, the gradient length on axis one is 3.083 s.d. and the two most distant site points on the axis, MLA and PVF, did have two species in common but both were at very high abundance at MLA and

low abundance at PVF. The length of this gradient also indicates whether it is appropriate to apply a linear or a unimodal model to the data. When the gradient is less than three standard deviations, a linear ordination method should be applied and when it is greater than four standard deviations, a unimodal model should be applied. Between three and four standard deviations, either method may be appropriate (ter Braak & Šmilauer 1998, p.37). The unimodal model of DCA was accepted here because the gradient just exceeded the minimum length, because it was expected that the species were responding unimodally to the environment and because the unimodal method can be more appropriate when there are many zeroes in the data as was the case in this data set (ter Braak & Šmilauer 1998, p.86).

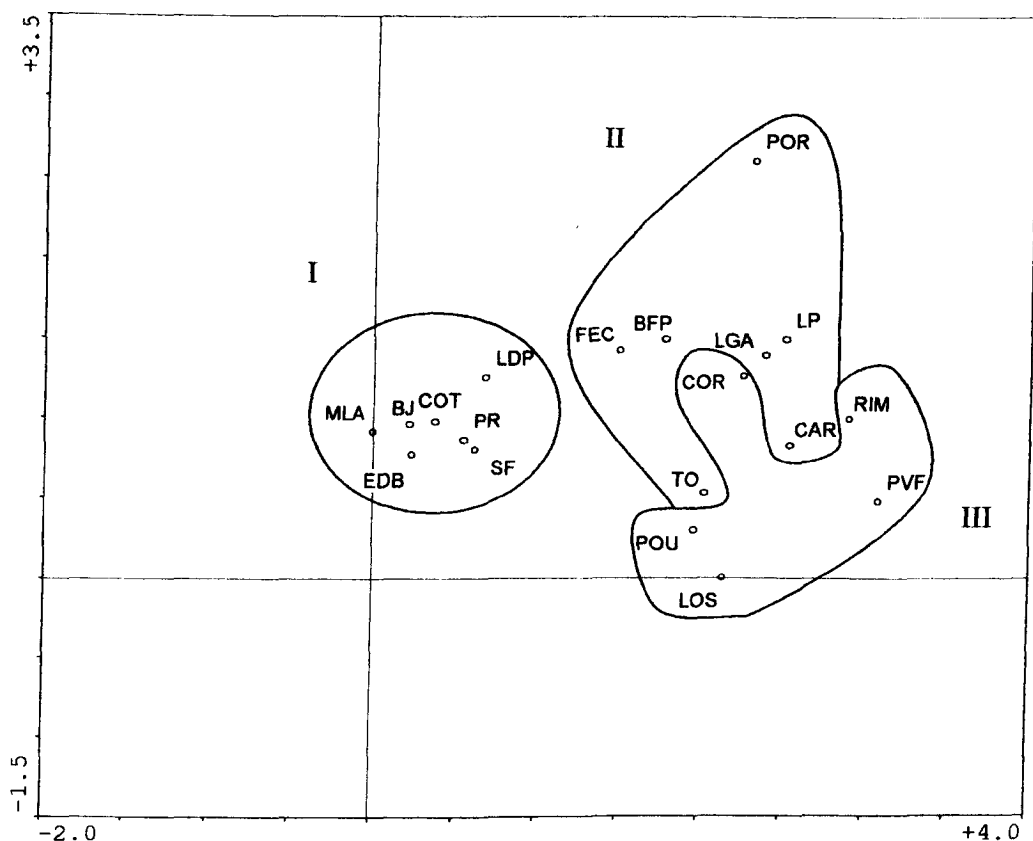


Figure 2.7 DCA site ordination of 19 sites sampled in 2000 (RPM deleted from analysis). Axis 1 eigenvalue = 0.594, axis 2 eigenvalue = 0.247. Site codes are explained in Table 2.1. TWINSpan groups I, II and III are encircled.

The effectiveness of the constructed ordination axes in explaining the species data is indicated by their eigenvalues. In the ordination of the 2000 species data, the eigenvalues of axis one and axis two were 0.594 and 0.247 respectively. These figures indicate that the ordination was explaining the species data reasonably well.

During the analysis, further axes were extracted from the data, each uncorrelated with the earlier axes and representing only previously unexplained variation. Ideally, the first two axes, which can be illustrated easily, explain the greatest amount of variation in the species data with each additional axis resulting in only a little more variation being explained. In this case, axis one explained 23.2% of the total amount of variation explained by the ordination. Axes one and two together explained 32.8%. By increasing the number of axes to three or four, the amount of variation explained was increased only a little to 37.4% or 39.9%. By focusing on only the first two axes, an ordination diagram is much easier to interpret and little information is lost.

In the site ordination diagram, the site groupings obtained from TWINSpan analysis are encircled (Figure 2.17). TWINSpan uses the same algorithm as DCA, identifying cut-off points on the axes at which divisions are made between groups of sites. By overlaying the groups on the diagram, the relationship between them, and between the individual sites within them, becomes apparent. For most of the sites, the TWINSpan groups clearly correspond with the positioning of the site points. However, the position of COR suggests that it should be in group II rather than group III. The species assemblage at this site was intermediate between the assemblages characteristic of each group. *E. azurea* was abundant, suggesting a similarity with group II, but *E. najas* was also present, suggesting a similarity with group III. TWINSpan analysis of all the species data placed COR in group III.

Relationships of species distributions with gradients in vegetation and environmental variables

The ordination diagram illustrates the observed spatial variation in species data using its artificial gradients. However, these gradients may reflect the real causative combination of environmental, biotic and chance factors which produces the observed species assemblages. Important environmental influences on plant distribution can be investigated by looking for associations between environmental variables measured at the survey sites and the ordination axes. This approach is described as indirect gradient analysis.

Correlation analysis (Spearman rank correlation coefficients) of the 2000 site scores on the ordination axes with the environmental variables measured at each site showed that the DCA gradients were associated with real environmental gradients (Table 2.23). Water depth decreased from left to right along axis one while sediment calcium content increased up axis two. These patterns suggested that sites closer to the left of the diagram could be expected to have deeper water and those at the right shallower water, while sites near the

bottom of the diagram could be expected to have sediment with a lower calcium content than those at the top.

Table 2.23 Significant ($p \leq 0.05$) Spearman rank correlation coefficients (r) between 2000 DCA axis site scores and environmental, vegetation and dominant trait variables.

Axis	Variable	Spearman r	P
Axis 1	Water depth	-0.487	0.034
	Species richness	-0.591	0.008
	Canopy height	-0.493	0.032
Axis 2	Sediment Ca	0.544	0.016
	Species richness	-0.506	0.027
	% canopy cover	-0.498	0.030
	Total root weight	0.493	0.032

The responses of individual species to these environmental gradients were considered by looking at the species ordination diagram (Figure 2.8). In a species ordination, each point represents that species' optimum values on the ordination gradients as calculated by the two-way weighted averaging algorithm. Species with similar optima will be close together on the diagram and are likely to co-occur in the field. In the species ordination diagram, the life-form of each species is indicated so that it can be seen clearly that the free-floating species are positioned at the left hand side, the emergent species in the middle and the submerged species at the right hand side. The association of water depth with axis one indicates that the free-floating species tended to occur in deep water and the submerged species in shallow water while the emergent species were found in intermediate to deep water. This pattern suggests that the distribution of species was not strongly influenced by hydrosere factors. If the distribution of the floating, submerged and emergent plants was caused by successional processes, then submerged species would be expected to occur in the deepest water, the floating species in intermediate water depths and the emergent species in the shallowest water. The distribution of the life-forms may have been more concerned with photosynthetic requirements of the different species. The importance of shallow water to the submerged species is probably linked to their requirement for sufficient levels of photosynthetically active radiation at the sediment where they may be rooted. Similarly, *Nymphaea* may depend on these conditions during growth of new leaves from the rhizome up through the water column before they reach the surface where they float. The free-floating plants do not have the challenge of underwater photosynthesis and they may benefit from a deeper water column, giving more room for root expansion. The reduced occurrence or abundance of the elsewhere dominant *E. azurea* at these sites may

have been because the young plants develop on the sediment surface and so initially photosynthesise underwater. Its reduced dominance may have removed a competitive pressure from the free-floating species allowing them to develop more successfully.

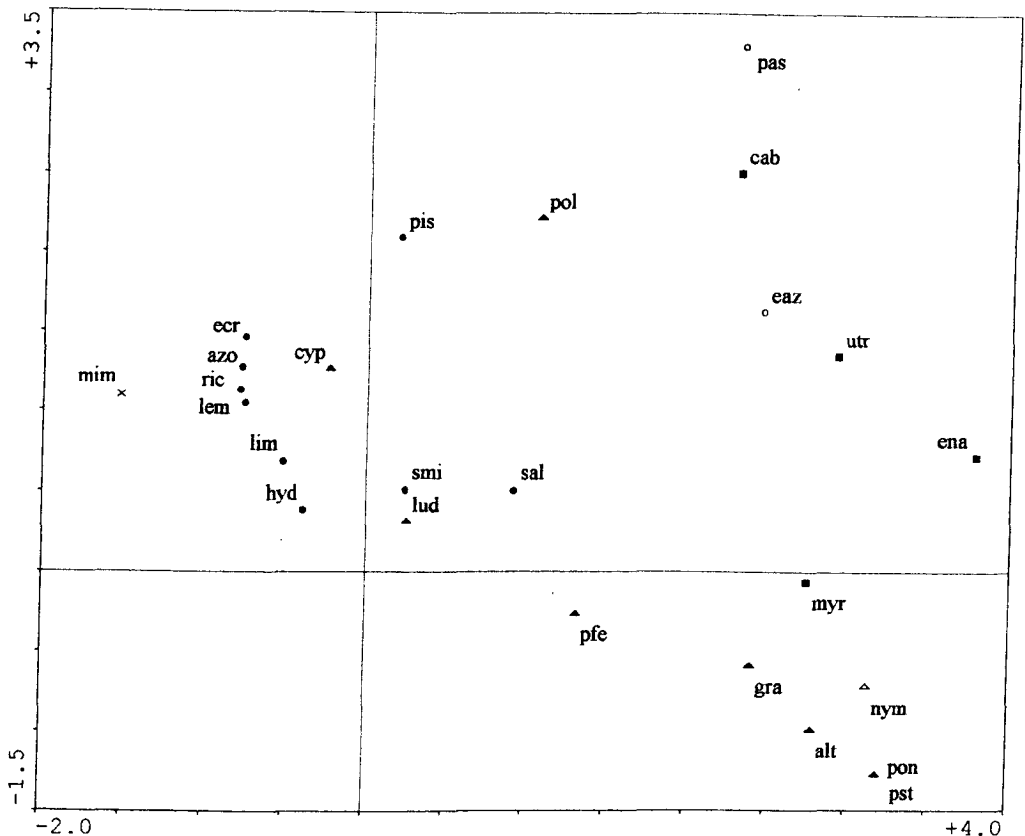


Figure 2.8 DCA species ordination of 2000 data (RPM, *Najas* sp. and *Nitella* sp. deleted from analysis). Axis 1 eigenvalue = 0.594, axis 2 eigenvalue = 0.247. azo *Azolla filiculoides*; alt *Alternanthera*; cab *Cabomba* sp.; cyp *Cyperaceae*; eaz *Eichhornia azurea*; ecr *Eichhornia crassipes*; ena *Egeria najas*; gra *Poaceae*; hyd *Hydrocotyle ranunculoides*; lem *Lemnaceae*; lim *Limnobium laevigatum*; lud *Ludwigia* sp.; mim *Mimosa pigra*; myr *Myriophyllum aquaticum*; nym *Nymphaea amazonum*; pas *Paspalum repens*; pis *Pistia stratiotes*; pfe *Polygonum ferrugineum*; pol *Polygonum* sp.; pst *Polygonum stelligerum*; pon *Pontederia cordata*; ric *Ricciocarpus natans*; sal *Salvinia* sp.; smi *Salvinia minima*; utr *Utricularia foliosa*. Filled circles = free-floating species, filled squares = submerged species, filled triangles = emergent species, open circles = bank-rooted, floating stems, open triangles = bottom-rooted, floating leaves.

Patterns of vegetation characteristics and dominant species traits across the sites and species were also examined by correlation analysis. Species richness was negatively correlated with both axis one and axis two indicating a diagonal decline in species richness from the bottom left towards the top right of the diagram. In relation to the environmental variables, this suggested lower species richness in shallower water and when sediment calcium was high. Canopy height (measured above the sediment and therefore related to water depth) decreased up axis one as did percentage canopy cover. Vegetation at sites at the top of the diagram was closer to the sediment and had a smaller canopy area than

vegetation at the sites at the bottom of the diagram. Root weight was the only trait of the dominant species to be correlated with any axis and it increased up axis two.

A full illustration of the sites by species data is provided by the joint plot of both site and species points (Figure 2.9). This is a major function of ordination analysis. This scatter of points within a two-axis space provides a summary of the relationships inherent in the dataset from which it is much easier to extract information than the two-way raw data matrix. In this diagram, the species points are located close to their optima on the two constructed axes. The site points are at the centroid of the species recorded at them, weighted by their abundance in this case. The diagram therefore can be used to interpret the likely species composition of each site using the centroid rule. Species encountered within a small radius of a site point most likely occurred there, and at high abundance. The larger the radius considered, the less likely that the species occurred, or if they did, the lower the abundance. The ranked likelihood of occurrence, or level of abundance, can be estimated by assessing the distance from a site point to the surrounding species points. For example, it would be predicted from this plot that the assemblage at PVF probably included *Utricularia foliosa* (utr), *Egeria najas* (ena) and *Myriophyllum aquaticum* (myr) at reasonable abundance, but was less likely to include *Polygonum ferrugineum* (pfe) and probably not *Eichhornia crassipes* (ecr). In fact, *Utricularia foliosa* (utr) did not occur at PVF, but it is very rare across the whole data set, and each of the other predictions was accurate.

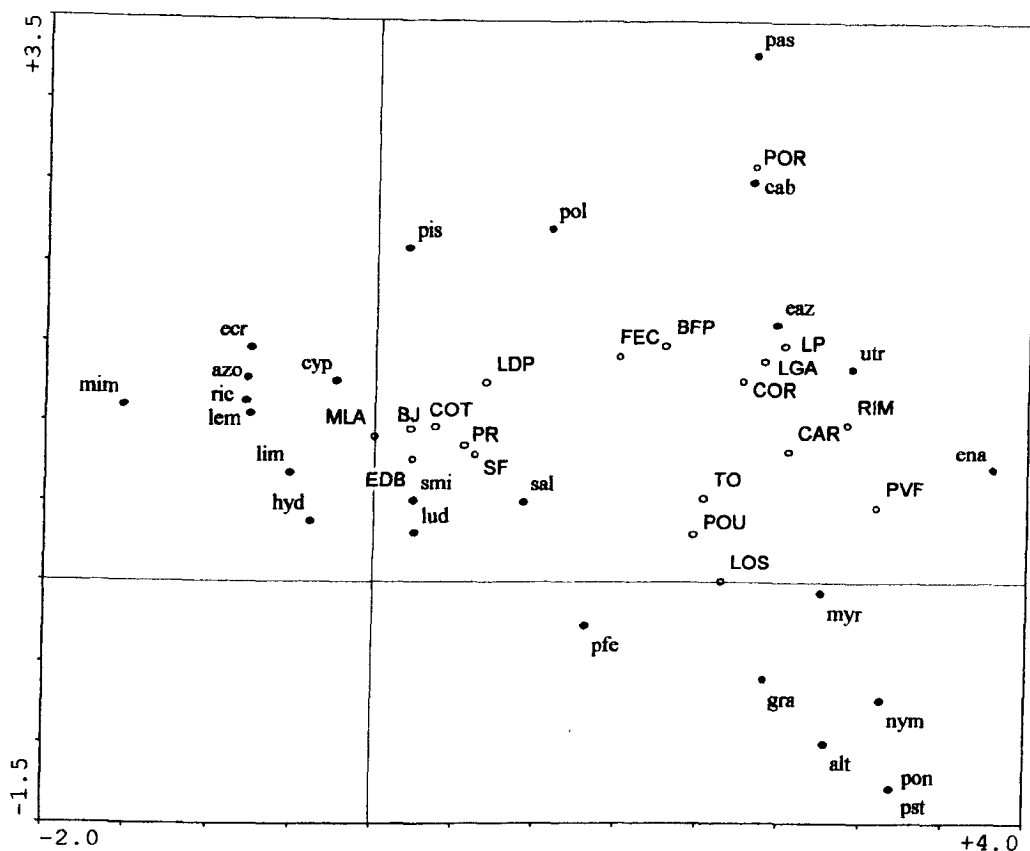


Figure 2.9 DCA ordination of 2000 sites and species data (RPM, *Najas* sp. and *Nitella* sp. deleted from analysis). Axis 1 eigenvalue = 0.594, axis 2 eigenvalue = 0.247. Site codes are explained in Table 2.1 and species codes in Figure 2.8.

2001 DCA

As in the DCA of the 2000 data set, the results of initial analysis of the 2001 data also focused on the major contrast between submerged plant communities and communities of mixed life-forms. Four of the sites associated with the main channel of the Paraná were represented by one point at the far right hand side of the site ordination while the remaining nineteen sites were distributed on axis two. Again the distinct environmental conditions in the main Paraná River channel explained the strongly contrasting species assemblage at these sites. The four sites, PVF2, RPM2, ISL and COR2, were made supplementary in subsequent analyses meaning that they were not used to construct the DCA axes. With this strong influence on the analysis removed, the DCA showed the relationships between the nineteen sites (Figure 2.10). The gradient length of axis one was slightly longer than in the 2000 DCA at 3.582 units, indicating that the unimodal model was suitable. There was complete species turnover across the diagram. VEN at the left hand side shared no species with the cluster of sites at the right hand side (BIL, LP2, GER,

BFP2, SUM). The eigenvalues showed that the ordination diagram was explaining the variation in the species data well. Axis one had an eigenvalue of 0.554 and explained 21.3% of the total variation explained by the ordination. Axis two had an eigenvalue of 0.368 and axes one and two together explained 35.6% of the total variation accounted for by the ordination. After four axes, the percentage variation explained rose to only 42.3% showing that the additional axes were not individually providing much new information.

The site ordination showed a few outlying sites. The site point for CAP was located at the far top right of the diagram. This site was unusual because there was very little macrophyte growth and only one *Nymphaea amazonum* plant was recorded. The water here was particularly cloudy due to suspended sediment. The site points for VEN and ONC were located at the far left hand side of the diagram. Both sites were dominated by *Eichhornia crassipes*, which was abundant at very few sites, with little other vegetation present.

The TWINSPAN groups are overlaid on the site ordination diagram (Figure 2.10). There appears to be a diagonal transition between groups from the top left to the bottom right. The wide scatter of points in TWINSPAN group II indicates that there was more variation within this group than within groups I or II.

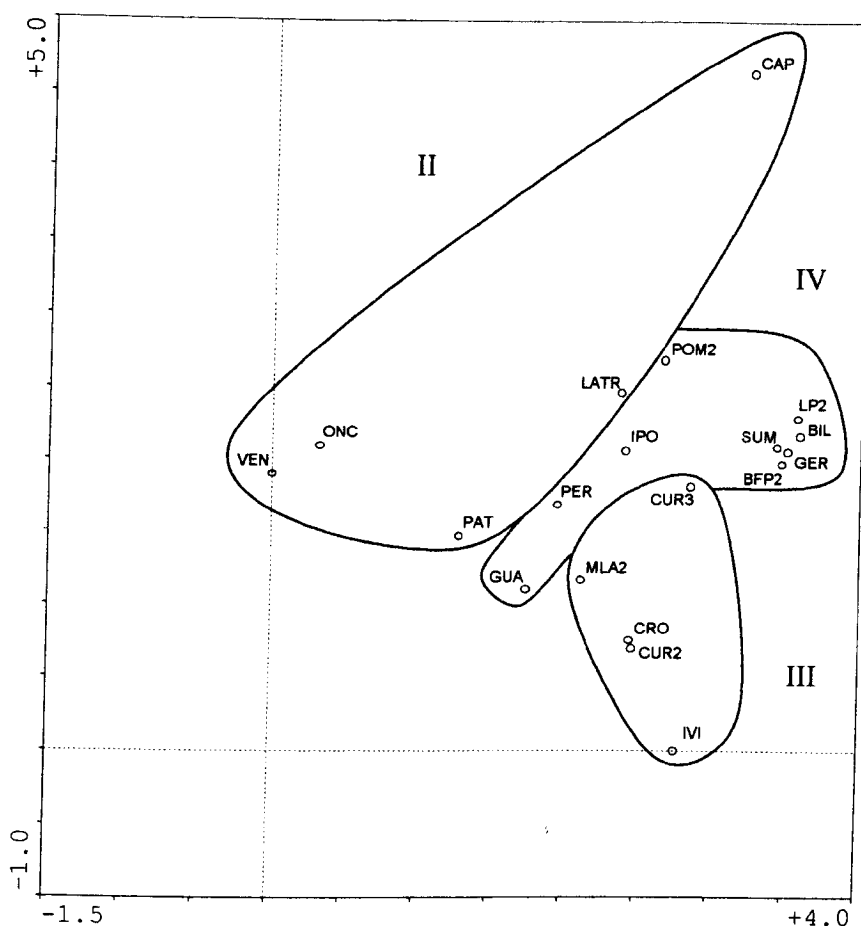


Figure 2.10 DCA site ordination of 19 sites sampled in 2001 (COR2, ISL, PVF2 and RPM2 supplementary). Axis 1 eigenvalue = 0.554, axis 2 eigenvalue = 0.368. Site codes are explained in Table 2.1. TWINSpan groups II, III and IV are encircled.

Relationships of species distributions with gradients in vegetation and environmental variables

Significant Spearman correlations between 2001 DCA axis scores and environmental and vegetation variables are shown in Table 2.24. Axis one was significantly positively correlated with sediment iron content indicating that this variable increased from sites at the left of the diagram towards sites at the right. Although the relationship was not quite statistically significant for axis one ($r = 0.445$, $p = 0.056$), water conductivity seemed to be positively correlated with both axis one and axis two indicating a diagonal increase in this variable from the bottom left to the top right of the diagram. Correlations of the axes with collective vegetation variables and dominant species trait variables were also found. In the 2001 data set, canopy cover and species richness were negatively correlated with both axis one and axis two, suggesting a gradient decreasing from sites at the bottom left to sites at the top right of the diagram. This direction in the diagram was also associated with increasing water conductivity. Canopy height and stem density decreased going up axis two. Biomass decreased along axis one in the same direction as the increase in sediment

iron content. Axis one was also associated with increasing stem length, remainder weight and leaf to root weight ratio of the dominant species.

Table 2.24 Significant Spearman rank correlation coefficients (r) between 2001 DCA axis site scores and environmental, vegetation and dominant trait variables.

Axis	Variable	Spearman r	p
Axis 1	Sediment Fe	0.596	0.007
	% canopy cover	-0.549	0.015
	Biomass	-0.653	0.002
	Species richness	-0.650	0.003
	Max. stem length	0.843	<0.001
	Remainder weight	0.674	0.002
	Leaf weight/root weight	0.529	0.052
Axis 2	Water conductivity	0.467	0.044
	% canopy cover	-0.605	0.006
	Stem density	-0.716	0.001
	Species richness	-0.594	0.007

Species ordination

By examining the species ordination diagram (Figure 2.11), the associations of individual species with the gradients in environmental conditions and vegetation structure were identified. For example, *Eichhornia azurea* (eaz) and *Cyperus* sp. (cyp), located towards the top right of the scatter, were associated with high water conductivity and with vegetation communities of low species richness and canopy cover. In contrast, *Eichhornia crassipes* (ecr) and *Polygonum ferrugineum* (pfe) were associated with low water conductivity and were likely to occur in species assemblages of high diversity and canopy cover. The role of *E. crassipes* in this community in its native habitat contrasts with the effect that it can have when it is introduced to new environments and may cause weed problems by massive, rapid proliferation (Pieterse & Murphy 1990).

It was not possible to make simple interpretations of all the points in the diagram. Some of the furthest outlying points represented species that were rare in the data set and were only recorded at sites with extreme environmental conditions. Without a reasonable number of occurrences, it was not possible to assess whether these sites were providing optimum conditions for these species or if the conditions were at the limits of their tolerance. There was a similar problem with interpreting points at the centre of the scatter. They may have been located here because the species they represented were responding unimodally to the axes and did in fact have their optima at the centre of the scatter. However, points could

also appear in this position if the species were responding bimodally, or if they were unrelated to the axes.

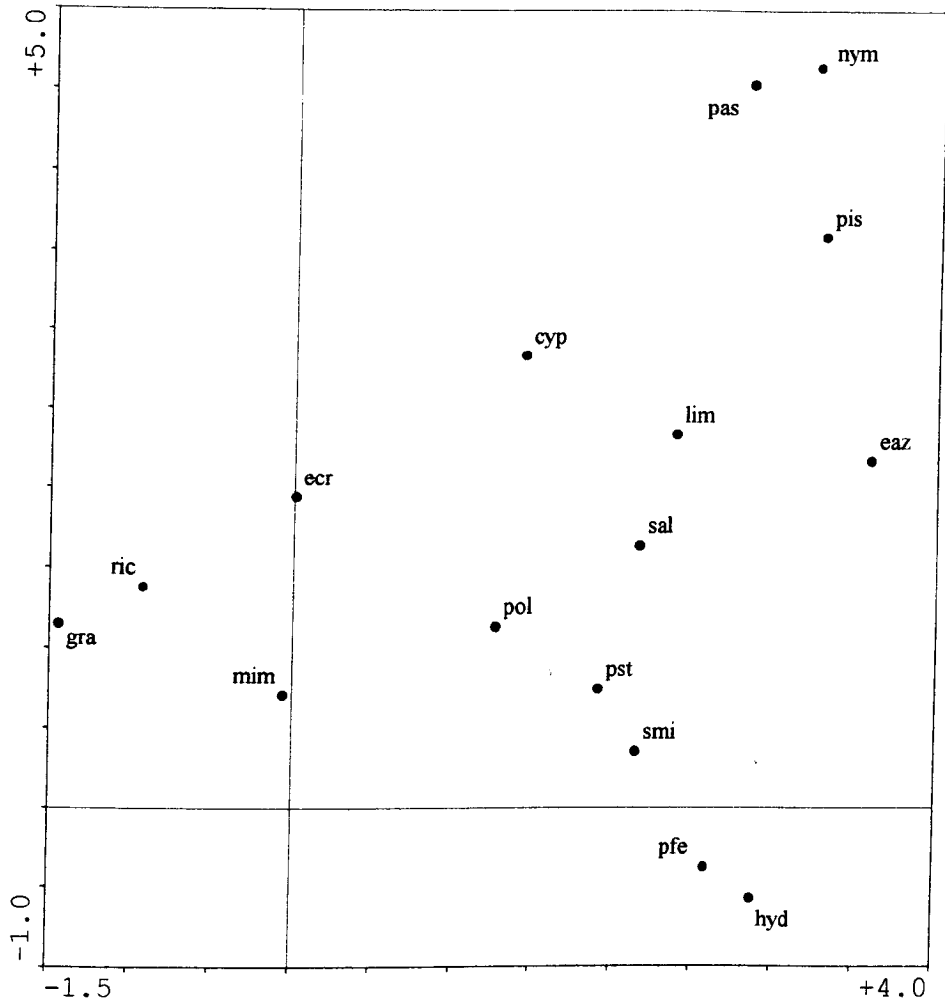


Figure 2.11 DCA species ordination of 2001 data (COR2, ISL, PVF2 and RPM2 supplementary). Axis 1 eigenvalue = 0.554, axis 2 eigenvalue = 0.368. cyp Cyperaceae; eaz *Eichhornia azurea*; ecr *Eichhornia crassipes*; gra Poaceae; hyd *Hydrocotyle ranunculoides*; lim *Limnobiium laevigatum*; mim *Mimosa pigra*; nym *Nymphaea amazonum*; pas *Paspalum repens*; pis *Pistia stratiotes*; pfe *Polygonum ferrugineum*; pol *Polygonum* sp.; pst *Polygonum stelligerum*; ric *Ricciocarpus natans*; sal *Salvinia* sp.; smi *Salvinia minima*.

The joint plot of sites and species again provides an illustration of the data set and a summary of the estimated species composition at each site (Figure 2.12).

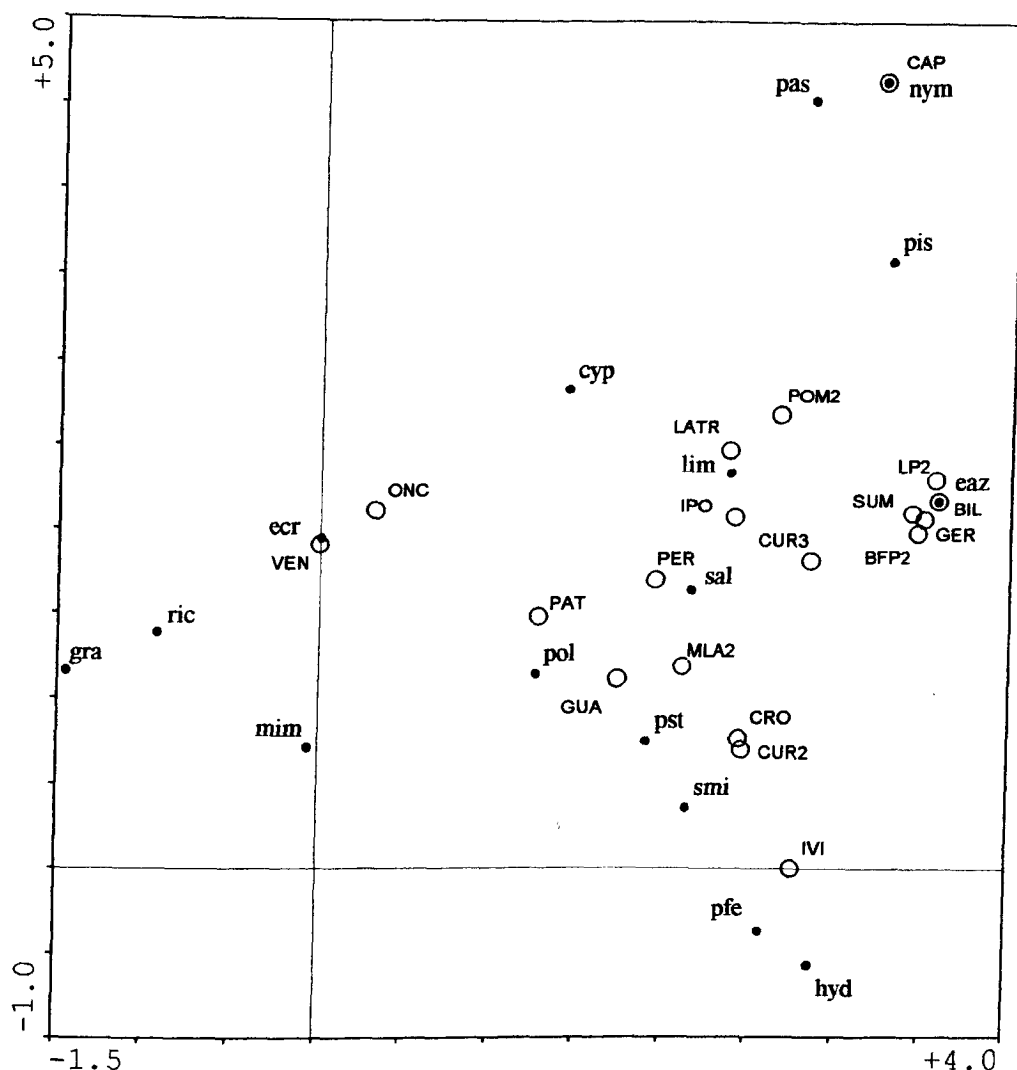


Figure 2.12 DCA ordination of 2001 sites and species data. Axis 1 eigenvalue = 0.554, axis 2 eigenvalue = 0.368. Site codes are explained in Table 2.1 and species codes in Figure 2.11.

2000-2001 DCA

In the separate ordination analyses of the two single year data sets, a small number of sites (one in 2000 and four in 2001) were so different from the others that little other information was shown in the diagrams. However, when the data sets from both years were combined to make one large data set, the site ordination was much more informative showing the relationships between all sites and a more gradual species turnover from left to right (Figure 2.13). The larger sample size resulting from the combination of the two data sets included more of the variation in species composition which occurs across different sites in the floodplain so that a continuum of vegetation change was seen rather than a simple division into sites supporting only submerged species and sites supporting a mixture of growth forms.

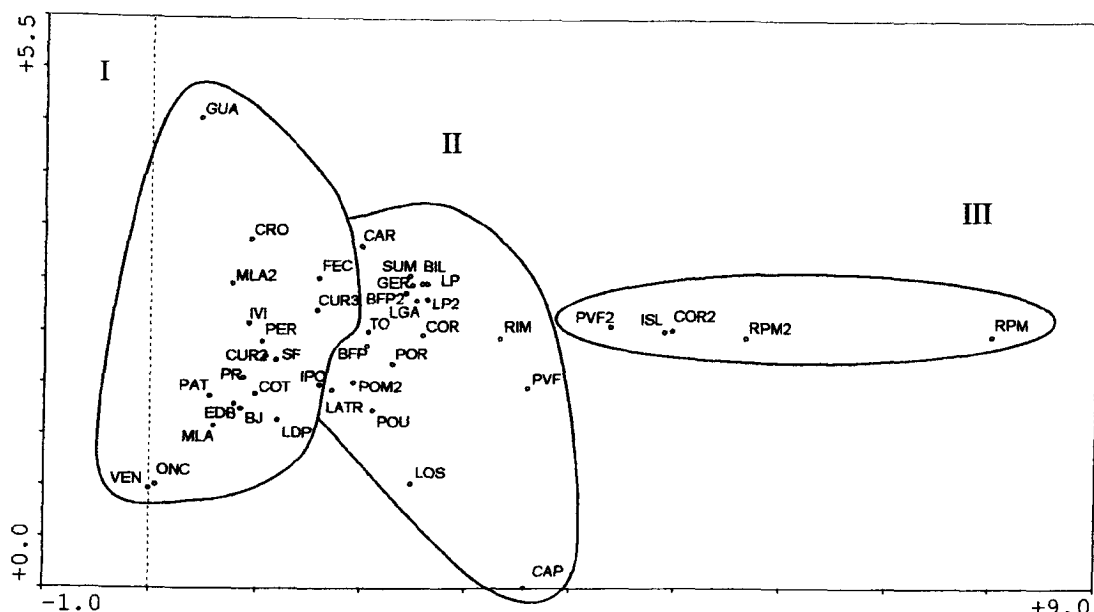


Figure 2.13 DCA site ordination of all sites sampled 2000-2001. Axis 1 eigenvalue = 0.837, axis 2 eigenvalue = 0.358. Site codes are explained in Table 2.1. TWINSpan groups I, II and III are encircled.

The large amount of species turnover in the ordination was indicated by the very long gradient of the first axis of 8.006 standard deviations. The species were responding unimodally to the artificial gradient and so the DCA method was appropriate for the data. The large eigenvalues (0.837 for axis one and 0.358 for axis two) were a reflection of the contrast between the submerged communities and others. The ordination was explaining this feature of the species data well, but further patterns in the sites with non-submerged communities were studied in a subsequent analysis in which the five most unusual sites were made supplementary. The first ordination axis explained 17.5% of the total amount of variation explained by the ordination, and the first and second axes together explained 25%. The percentage variation explained rose to 30.5% after three axes and 34.1% after four axes. The first two illustrated axes were the most informative as in the previous analyses.

The three TWINSpan groups extracted from the 2000-2001 data set are outlined in the site ordination diagram. The groups are arranged along axis one with TWINSpan group I, in which free-floating species were particularly abundant, on the left hand side, TWINSpan group II, in which *Eichhornia azurea* was highly dominant, in the middle and TWINSpan group III, formed entirely by sites supporting only submerged species, at the right hand side.

Relationships of species distributions with gradients in vegetation and environmental variables

There were significant correlations between the site scores on the ordination axes and environmental variables, collective vegetation characteristics and dominant species traits (Table 2.25). Water pH and conductivity, sediment pH and the degree of light penetration through the water column (Z_{eu}/d) all increased from left to right along axis one. Water depth and the light extinction coefficient decreased in the same direction. Axis two represented a gradient of increasing water phosphorus concentration and sediment nitrogen and calcium concentration and decreasing water depth. The negative correlation of water depth and species richness with both axis one and axis two indicated a diagonal decrease in both variables from the bottom left of the diagram towards the top right. Canopy cover was significantly correlated with axis two, and its correlation with axis one was close to significance ($r = -0.294$, $p = 0.059$) so this variable may also have been decreasing diagonally from the bottom left to the top right. Canopy height and biomass decreased from left to right along axis one and the leaf weight to root weight ratio increased. Axis two was associated with increasing stem length and remainder weight of the dominant species from the bottom to the top.

Table 2.25 Significant Spearman rank correlation coefficients (r) between 2000-2001 DCA axis site scores and environmental, vegetation and dominant trait variables.

Axis	Variable	Spearman r	p
Axis 1	Water depth	-0.298	0.052
	k	-0.383	0.013
	Z_{eu}/d	0.476	0.002
	Water pH	0.441	0.003
	Water conductivity	0.453	0.002
	Sediment pH	0.321	0.036
	Canopy height	-0.570	<0.001
	Biomass	-0.676	<0.001
	Species richness	-0.589	<0.001
	Leaf weight/root weight	0.350	0.033
Axis 2	Water depth	-0.339	0.026
	Water P	0.323	0.034
	Sediment N	0.338	0.026
	Sediment Ca	0.388	0.010
	% canopy cover	-0.377	0.014
	Species richness	-0.345	0.024
	Max. stem length	0.412	0.007
	Remainder weight	0.467	0.005

Species ordination

By indicating these gradients on the species ordination, the associations of particular species with environmental, collective vegetation and dominant species traits can be interpreted (Figure 2.14). The species ordination shows the turnover from free-floating species at the left of the diagram towards emergent species and bank-rooted, stoloniferous species (*E. azurea* and *Paspalum repens*) in the middle, and submerged species at the right. The submerged species were therefore associated with shallow, clear water with good light availability at the bottom, high water pH and conductivity and high sediment pH. Biomass, canopy height, percentage canopy cover and species richness of the submerged communities tended to be low and the leaf weight to root weight ratio of the dominant species was high. There was little overlap between submerged and emergent or stoloniferous life-forms in the diagram indicating that they did not often co-exist. The species point for *Eichhornia azurea* (eaz) was close to the submerged species points. The seedlings of *E. azurea* develop underwater and so the species requires habitats that are suitable for submerged growth during the seedling phase, although the mature plant does not. *Nymphaea amazonum* (nym) was also close to the submerged species on axis one. This may be because it shares some requirements with submerged species, such as good underwater light availability, when new leaves grow up from the rhizome through the water column before reaching the surface where they float. The species point for *Myriophyllum aquaticum* (myr) is located at the boundary between submerged and emergent species. *Myriophyllum* has both emergent and submerged leaves, depending upon conditions, and so it can grow in habitats where either of these life-forms is favoured. In relation to axis two, the submerged species are in the middle suggesting either that they were favoured by intermediate water phosphorus and sediment nitrogen and calcium, or that these were not important variables influencing their distribution.

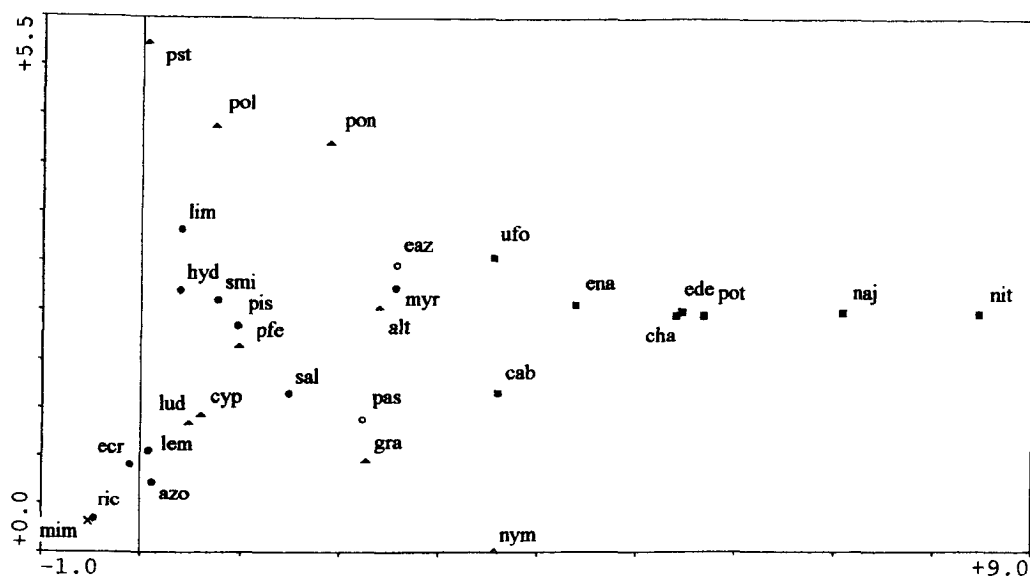


Figure 2.14 DCA species ordination of 2000-2001 data. Axis 1 eigenvalue = 0.837, axis 2 eigenvalue = 0.358. azo *Azolla filiculoides*; alt *Alternanthera*; cab *Cabomba* sp.; cha *Chara* sp.; cyp Cyperaceae; eaz *Eichhornia azurea*; ecr *Eichhornia crassipes*; ede *Egeria densa*; ena *Egeria najas*; gra Poaceae; hyd *Hydrocotyle ranunculoides*; lem Lemnaceae; lim *Limnobium laevigatum*; lud *Ludwigia* sp.; mim *Mimosa pigra*; myr *Myriophyllum aquaticum*; naj *Najas* sp.; nit *Nitella* sp.; nym *Nymphaea amazonum*; pas *Paspalum repens*; pis *Pistia stratiotes*; pfe *Polygonum ferrugineum*; pol *Polygonum* sp.; pon *Pontederia cordata*; pot *Potamogeton pusillus*; pst *Polygonum stelligerum*; ric *Ricciocarpus natans*; sal *Salvinia* sp.; smi *Salvinia minima*; utr *Utricularia foliosa*. Filled circles = free-floating species, filled squares = submerged species, filled triangles = emergent species, open circles = bank-rooted, floating stems, open triangles = bottom-rooted, floating leaves, x = terrestrial.

The free-floating species at the left hand side of the diagram were associated with deeper, less clear water through which less light reached the sediment, low water pH and conductivity and low sediment pH. The vegetation tended to be high above the sediment (the height measurement was related to water depth) with high percentage canopy cover, biomass and species richness. Leaf weight to root weight ratios of the dominant species were low. At the left of the diagram, species scatter on axis two was quite wide. Some of the species were rare in the data set and so their preferences could not be interpreted. However, the position of *Polygonum stelligerum* (pst) and *Polygonum* sp. (pol) towards the top of the axis suggested that they had higher optimum water phosphorus and sediment nitrogen and calcium requirements than *Eichhornia crassipes* (ecr), which was much lower down.

The joint plot of both species and sites illustrates the species data (Figure 2.15). The colour-coding of the site points in Figure 2.15 shows that species composition was related to the river with which the sites were associated. The blue site points, indicating sites that were associated with the Paraná River, are mainly located at the right hand side of the diagram. This largely reflects the importance of submerged species in the plant

communities found at Paraná sites. Points representing sites associated with the Baía River (red points), the Ivinheima River (green points) and Curutuba Channel (pink points) are located towards the left of the diagram. There is not a clear pattern separating species composition between these three channels. Bini *et al.* (2001) showed that species compositions in floodplain waterbodies tended to be more similar between sites associated with the same rivers than between sites associated with different rivers. The results presented here show that the Paraná River was associated with a distinctive vegetation type, but the Baía and Ivinheima Rivers were not. The reason for the importance of submerged species at sites associated with the Paraná River, resulting in a vegetation type that differs from those found on the Baía and Ivinheima Rivers, may be the stabilisation of water levels and increased water clarity which have resulted from increasing regulation of river flow by upstream dams, and the abundance of propagules of submerged species arriving from upstream reservoirs (Thomaz *et al.* 2004).

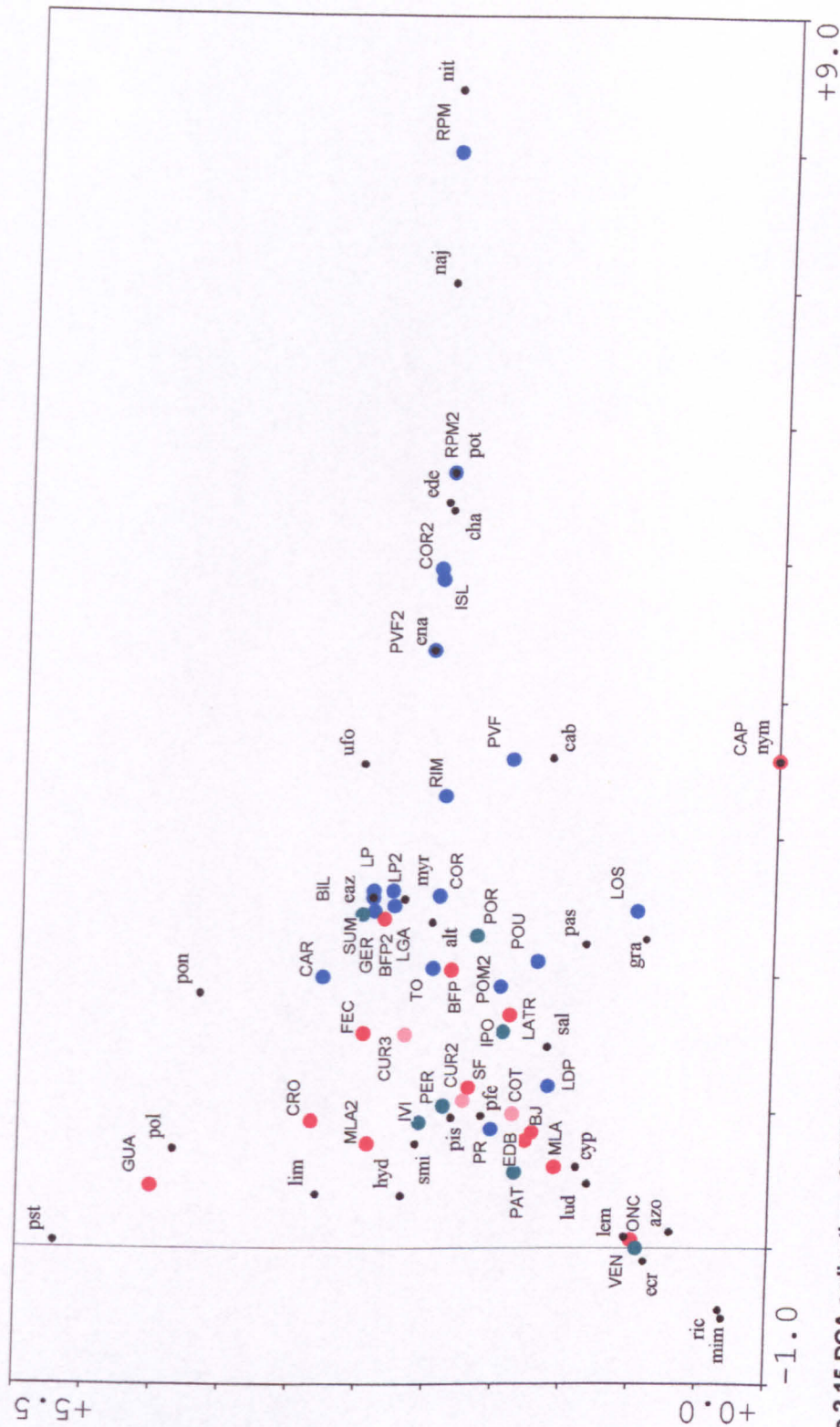


Figure 2.15 DCA ordination of 2000-2001 sites and species data. Axis 1 eigenvalue = 0.837, axis 2 eigenvalue = 0.358. Site codes are explained in Table 2.1 and species codes in Figure 2.14. Blue points indicate sites associated with the Paraná River; Red with the Ivinheima River; Pink with Canal Curutuba.

Five unusual sites made supplementary

When all 43 sites were analysed using DCA, the ordination was strongly influenced by the contrast of the submerged plant communities with other communities. The results were useful for illustrating the species variation observed across the sampling sites in the floodplain and for identifying the environmental gradients likely to be responsible for this variation, particularly factors necessary for submerged growth. By making the five sites that were separated in the first division of TWINSpan analysis supplementary, it was possible to study the relationships between the remaining 38 sites (Figure 2.16). The five sites, RPM, RPM2, PVF2, COR2 and ISL were not involved in construction of the ordination axes although three of them were plotted on afterwards.

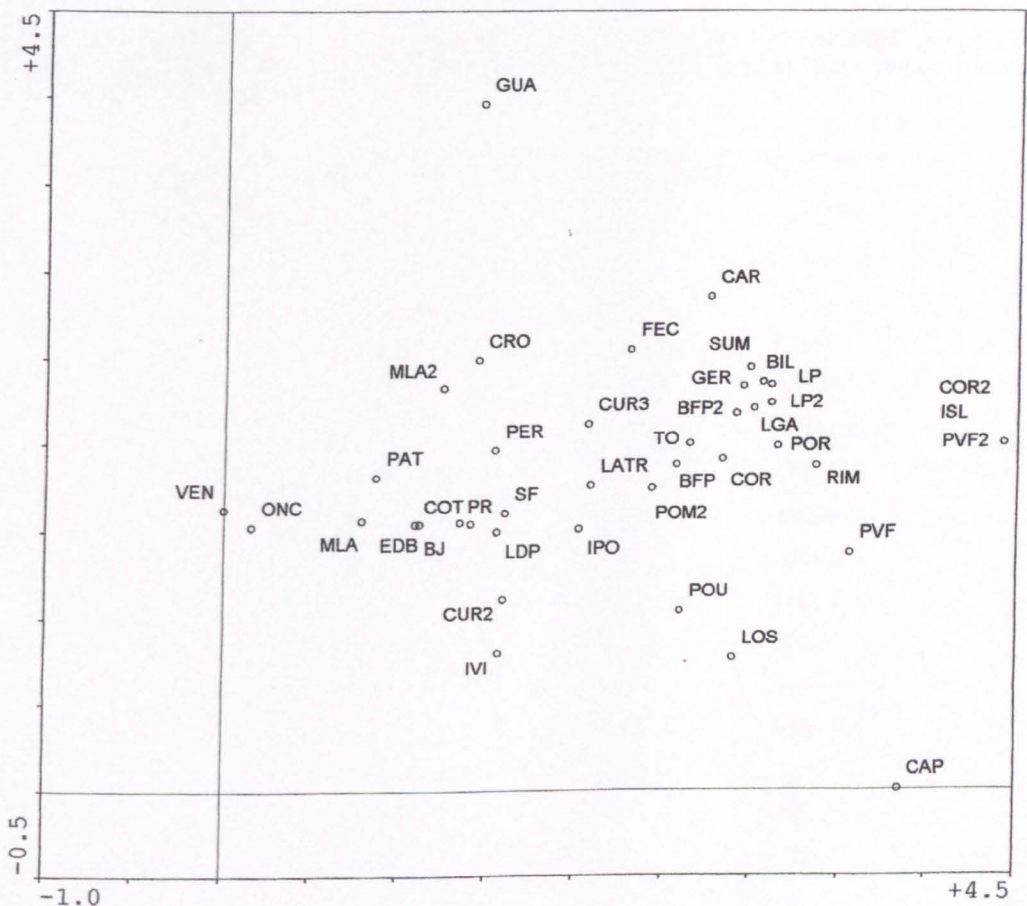


Figure 2.16 DCA site ordination of sites sampled 2000-2001 (COR2, ISL, PVF2, RPM, RPM2 supplementary). Axis 1 eigenvalue = 0.537, axis 2 eigenvalue = 0.325. Site codes are explained in Table 2.1.

The eigenvalues were 0.537 for axis one and 0.325 for axis two so the ordination explained the species data well. The gradient length for axis one was 3.845 confirming that the unimodal model was suitable. The first two axes accounted for the greatest amount of

variation in the species data explained by the ordination (28.7%), increasing to 36% after three axes and 40% after four axes.

The significant Spearman correlation coefficients between axis scores and environmental and vegetation variables are shown in Table 2.26. As before, axis one represented a gradient of increasing water conductivity and PAR availability at the bottom (but not water or sediment pH) and decreasing water depth. A negative correlation with k was not quite statistically significant ($r = -0.306$, $p = 0.058$). Axis one was associated with increasing leaf to root weight ratio of the dominant species as before, and in addition, increasing stem length of the dominant species and decreasing canopy height, canopy cover, biomass and species richness.

Table 2.26 Significant Spearman rank correlation coefficients (r) between 2000-2001 DCA axis site scores (COR2, ISL, PVF2, RPM, RPM2 deleted) and environmental, vegetation and dominant trait variables.

Axis	Variable	Spearman r	p
Axis 1	Water depth	-0.378	0.015
	Z_{sed}/d	0.492	0.001
	Water conductivity	0.408	0.008
	Canopy height	-0.508	0.001
	% canopy cover	-0.335	0.032
	Biomass	-0.634	<0.001
	Species richness	-0.582	<0.001
	Max. stem length	0.319	0.048
	Leaf weight/root weight	0.414	0.012
Axis 2	Water depth	-0.347	0.026
	Water P	0.355	0.023
	Sediment N	0.321	0.041
	Sediment Ca	0.321	0.041
	% canopy cover	-0.482	0.001
	Species richness	-0.352	0.024
	Total leaf weight	0.341	0.031
	Total leaf area	0.360	0.022
	Max. stem length	0.318	0.049
	Remainder weight	0.485	0.004
	Total plant weight	0.323	0.042

Axis two again represented gradients of increasing water phosphorus and sediment nitrogen and calcium and decreasing water depth. The stem length and remainder weight of the dominant species again increased and percentage canopy cover and species richness

decreased. There were additional gradients of increase in leaf weight, leaf area and total plant weight of the dominant species.

Water depth, canopy cover, species richness and stem length of the dominant species were each correlated with both axis one and axis two. Water depth, canopy cover and species richness therefore decreased diagonally from bottom left to top right while stem length of the dominant species increased.

Species ordination

In the species ordination, species points were well scattered over both axes, although some of the species around the edges of the scatter were rare (Figure 2.17).

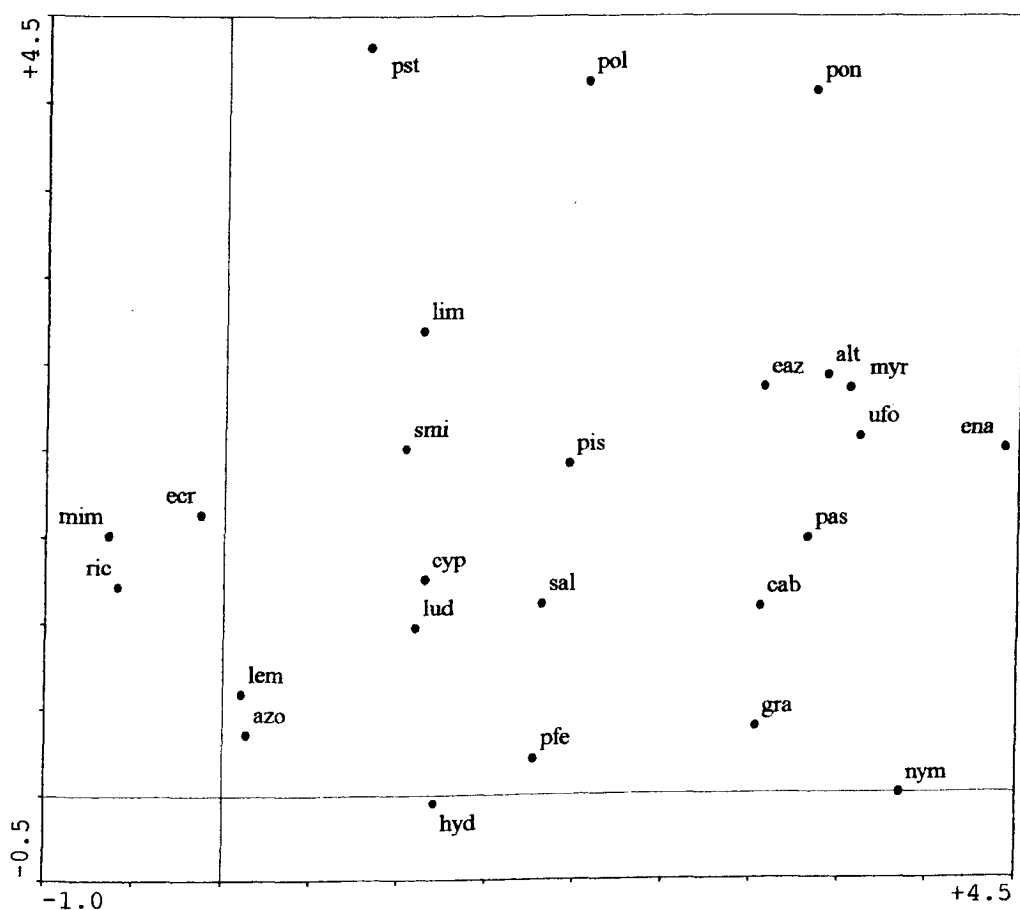


Figure 2.17 DCA species ordination of 2000-2001 data (COR2, ISL, PVF2, RPM and RPM2 supplementary). Axis 1 eigenvalue = 0.537, axis 2 eigenvalue = 0.325. Species codes are explained in Figure 2.14.

The submerged species were still at the right hand side of the diagram but they were not as well separated from the other species as in the earlier ordination. *Eichhornia azurea* (eaz) and *Paspalum repens* (pas), two bank-rooted, surface-floating stoloniferous species, were

close to the submerged species suggesting coexistence of the two life-forms. The emergent and some free-floating species were in the middle of the scatter. Small free-floating species may grow between the stems of emergent *Polygonum ferrugineum* (pfe) and *Polygonum* sp. (pol) while *Cyperus* sp. (cyp) may root in surface-floating mats of *Salvinia* sp. (sal). Most of the free-floating species were towards the left of the scatter.

Figure 2.18 shows the joint plot of both site and species points for the 2000-2001 data set with five sites made supplementary.

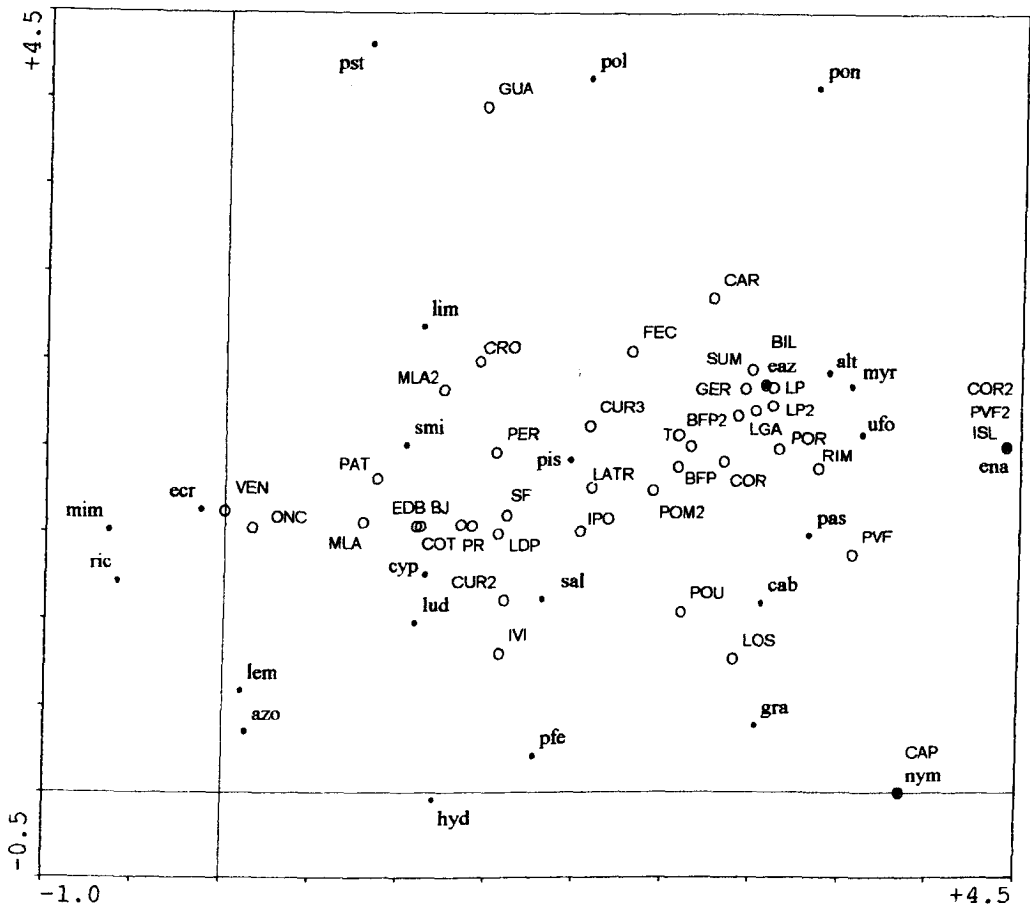


Figure 2.18 DCA ordination of 2000-2001 sites and species data (COR2, ISL, PVF2, RPM and RPM2 supplementary). Axis 1 eigenvalue = 0.537, axis 2 eigenvalue = 0.325. Site codes are explained in Table 2.1 and species codes in Figure 2.14.

Making the five unusual sites supplementary did not greatly affect the results of the ordination. The relative positions of the remaining sites were hardly affected and the associations between environmental variables and the axes were largely unchanged. Some additional patterns in dominant species trait variables were observed across the diagrams. In general, little new information was obtained by making the sites supplementary. The

DCA of all the sites was considered most interesting because it included the species variation across all of the vegetation communities that were observed in the floodplain.

CCA analysis of aquatic species data

2000 CCA

As in the DCA of these data, CCA separated RPM from all of the other sites, and the submerged species that grew there from all of the other species (Figure 2.19).

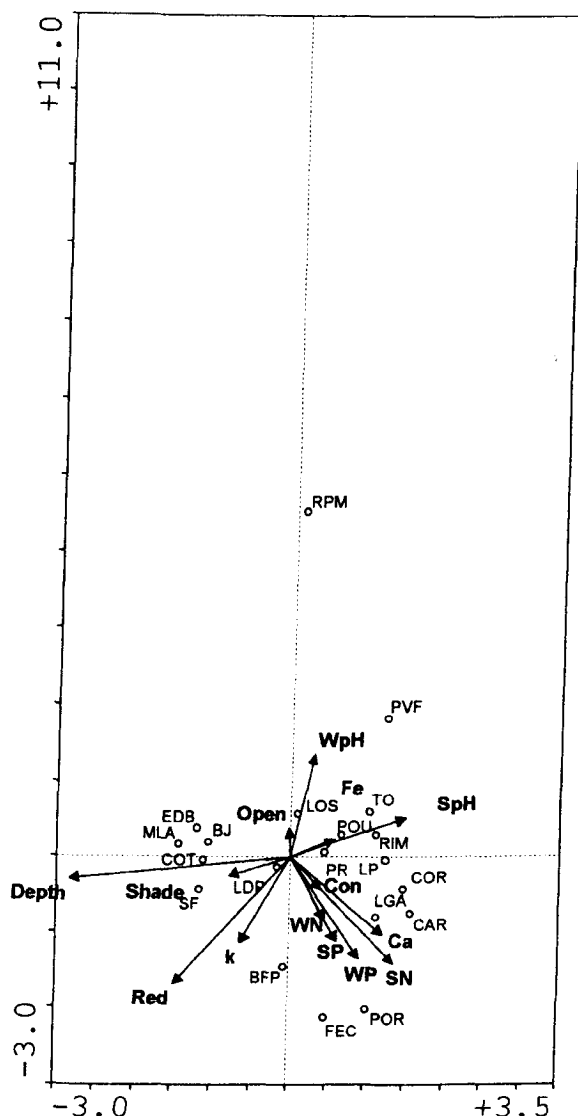


Figure 2.19 CCA site ordination of all sites sampled in 2000. Axis 1 eigenvalue = 0.509, axis 2 eigenvalue = 0.418. Site codes are explained in Table 2.1. Depth water depth; Open % sky obscured; WpH water pH; Fe sediment total Fe; SpH sediment pH; Con water conductivity; Ca sediment total Ca; SN sediment TKN; WP water total P; SP sediment ADAS extractable P; WN water TKN; k light extinction coefficient; Red sediment redox potential; Shade shade score.

The environmental conditions at RPM differed strongly from the other sites as well as its species composition. The separation was on axis two, which was most strongly correlated with sediment redox potential. The position of the RPM site point showed that it was associated with clear water of high pH and low in phosphorus, and less oxidised sediment low in nitrogen. It was not possible to predict the optimum conditions for the two species encountered at this site because they were not recorded anywhere else, but it makes sense that the clear water should favour their growth while the low sediment nitrogen could discourage growth of potential competitors.

The eigenvalues for this analysis were 0.509 and 0.418 for axis one and axis two respectively and the environmental data explained 60.7% of the species data. The relationship between the species data and the environmental variables was not statistically significant.

When RPM was made supplementary in the analysis, it became easier to interpret relationships between the remaining sites and species. The distribution of sites and species in the CCA (Figure 2.20) was very similar to their distribution in the DCA, indicating that the set of measured environmental variables was playing an important role in influencing species distribution.

Sample ordination

The TWINSpan groupings of sites were reasonably well maintained in the CCA sample ordination with group I appearing most distinct and groups II and III showing more overlap (Figure 2.20). Depth was strongly correlated with site axis position in the DCA ordination, and the direction of this gradient was apparent in the CCA ordination. It was very closely correlated with axis one and was shown to be the strongest explanatory variable of the species data, either on its own or in combination with other variables. Sediment redox potential and nitrogen content were also good individual explanatory variables. The light extinction coefficient (k) was not a good explanatory variable on its own, but as a second variable combined with water depth, it explained the greatest amount of additional, unique variation.

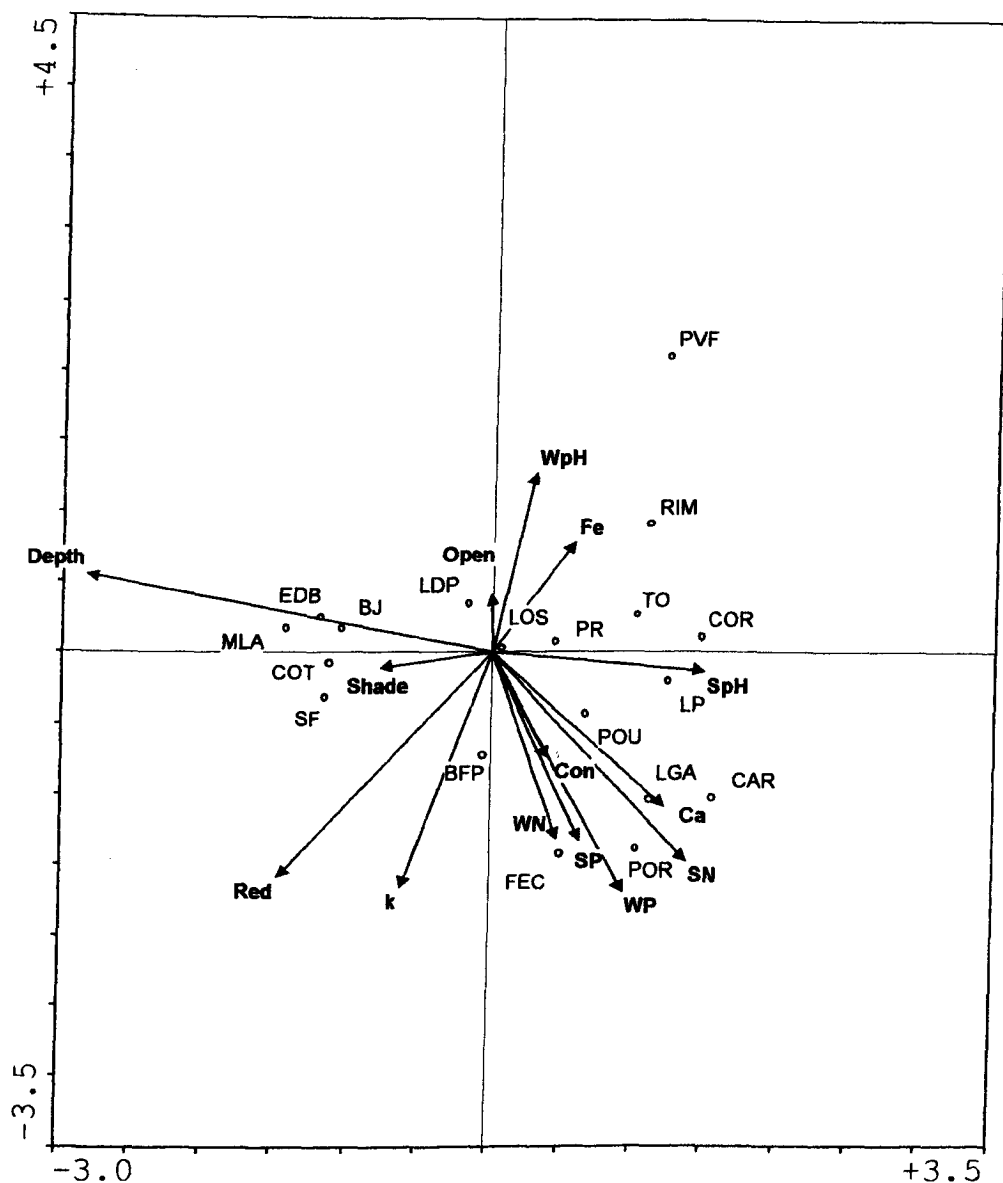


Figure 2.20 CCA site ordination of sites sampled in 2000 (RPM supplementary). Axis 1 eigenvalue = 0.509, axis 2 eigenvalue = 0.333. Site codes are explained in Table 2.1 and environmental variable codes in Figure 2.19.

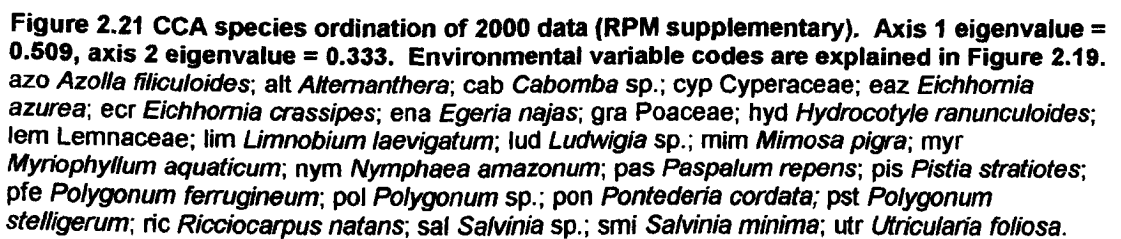
There were a few extreme values in the environment data (*e.g.*, sediment calcium at LGA and water nitrogen at CAR were particularly high) which would have had a strong influence in the regression but since they did not appear to be errors they were kept in the analysis. The variance inflation factors in the multiple regression equation for the environmental variables were all less than 20, indicating that each variable was explaining at least a small amount of variation which was not explained by any other variable (ter Braak & Šmilauer 1998). If a variance inflation factor for a particular variable is very large (> 20) then that variable is correlated with one or more other explanatory variables

and so is not making a unique contribution to the regression equation (ter Braak & Šmilauer 1998).

The site ordination diagram showed that TWINSPAN group I was associated with deep water that was relatively low in phosphorus, with more acidic sediment that was relatively low in nitrogen, phosphorus and calcium. TWINSPAN groups II and III were associated with shallower water and higher sediment pH. TWINSPAN group II sites had higher water conductivity, nitrogen and phosphorus and sediment nitrogen, phosphorus and calcium than group III. They also had more turbid water of lower pH, lower sediment iron and more oxidised sediment.

Species ordination

Life-forms were separated more distinctly than in the DCA diagram (Figure 2.21). The free-floating species were most clearly separated from the others at the deep end of the water depth gradient. Emergent and submerged species were both at the shallow end. These two groups were separated on axis two with submerged species towards the top and emergent towards the bottom. This was associated with strong gradients in sediment redox potential, light attenuation (k) and sediment and water nutrients. As expected, the submerged species were at the clearer water end of the k gradient and the species with aerial leaves at the more turbid end. Lower nutrients in the sediment may have made conditions too stressful for the emergent and stoloniferous species, many of which are large plants. However, the small, low biomass submerged species may have been able to exploit these areas due to their capacity to grow in nutrient-poor sediment and in response to release from any competitive suppression by the large emergent and stoloniferous plants. More oxygenated sediment seemed to favour the emergent and stoloniferous species while the submerged species also tolerated low sediment redox potential. The most frequently dominant species, *E. azurea*, was associated with shallow water and high sediment nitrogen, phosphorus and calcium and water nitrogen and phosphorus. *Paspalum repens*, which has a similar morphology of bank-rooted stems which float across the water surface with roots at internodes, was also associated with these conditions. *E. azurea* in particular is a high biomass species which could be expected to require a good nutrient supply.



The CCA diagrams explained the species data well with eigenvalues of 0.509 and 0.333 for axes one and two respectively. The first two illustrated axes provided a good representation of the whole ordination explaining 32.9% of the total variance in the species data and 41.7% of the total variance in the fitted values obtained by regression of the site

scores on the environmental variables. Overall, the environmental variables explained 78.8% of the total variation in the species data. However, Monte Carlo permutation tests showed that the species data were not significantly related to the environment.

2001 CCA

As in the DCA, the initial CCA separated some sites associated with the main channel of the Paraná (RPM2, ISL, COR2, and PVF2) and the submerged species they supported (*P. pusillus*, Charophyte, *Najas* sp., *E. densa* and *E. najas*) from all of the other sites and species (Figure 2.22). The environmental gradients on the diagram showed that these sites had unusually good light penetration to the sediment (high $Z_{eu/d}$) and high water conductivity. The eigenvalue for axis one was 0.954 and this was statistically significant indicating that the environmental data was explaining the contrast in species composition between sites in TWINSpan group I and all of the other sites. The eigenvalue of axis two was 0.432. The first two axes showed 33.6% of the total variance in the species data and 46.8% of the total variance in the fitted values after regression on the environmental variables. The environmental data explained 71.8% of the total variance in the species data.

Since the strong gradients associated with the main channel sites dominated the diagrams, the sites in TWINSPAN group I were made supplementary to allow CCA to detect more subtle patterns in the remaining data.

Sample ordination

The TWINSPAN groups were quite well preserved although there was overlap between all three (Figure 2.23). Water conductivity, sediment pH and site openness were the best single explanatory variables of the species data. Sediment iron was also useful for explaining additional variation when combined with water conductivity and openness. Although not the best explanatory variable this time, water depth still explained a relatively large amount of variation and was strongly correlated with axis two.

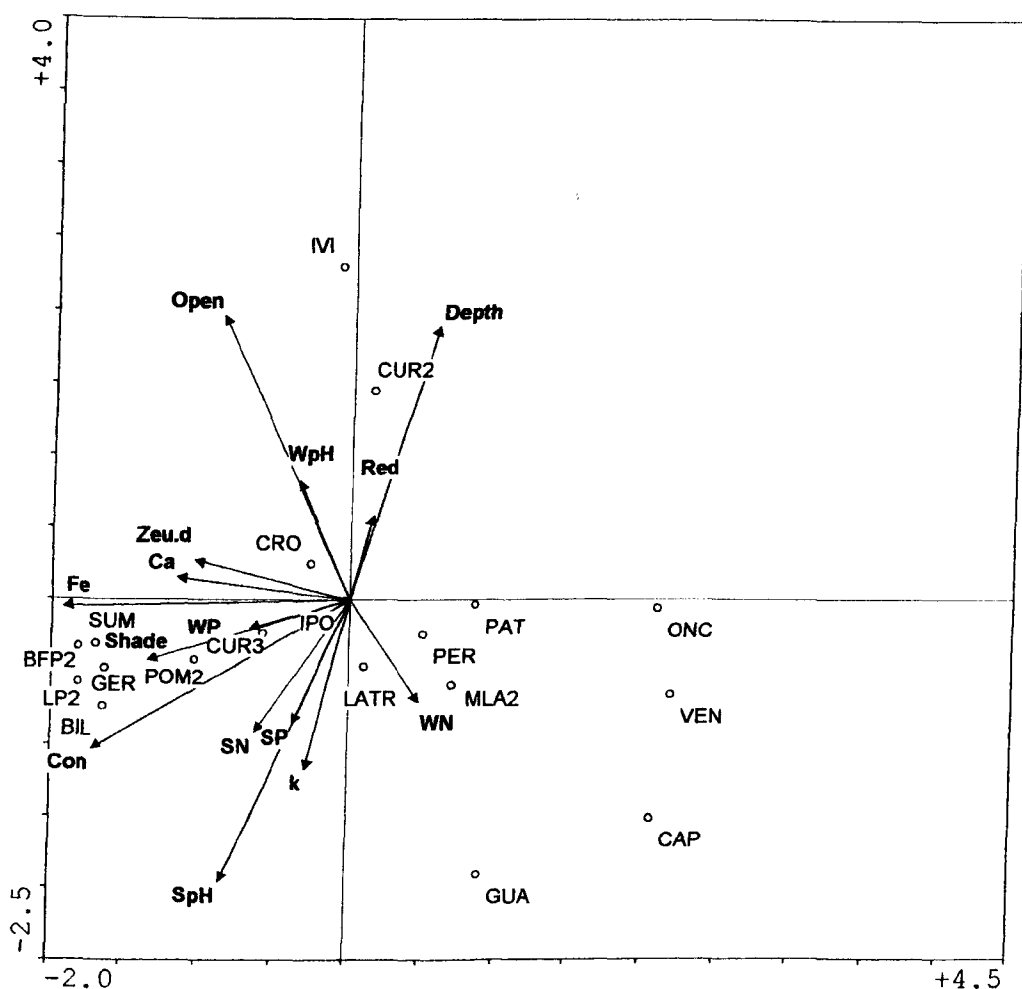


Figure 2.23 CCA site and environment biplot of 2001 data (COR2, ISL, PVF2, RPM2 supplementary). Axis 1 eigenvalue = 0.511, axis 2 eigenvalue = 0.443. Site codes are explained in Table 2.1 and environmental variable codes in Figure 2.19.

Sediment phosphorus, nitrogen, iron and calcium had very large variance inflation factors (> 40), indicating that they were correlated with other variables and were probably making

no unique contribution to the regression. Water depth and $Z_{eu/d}$ had variance inflation factors greater than 20, indicating that they were also contributing little. A few variables had extreme values (*e.g.*, the water was particularly deep at CUR2 and k was particularly high at GER) but again these did not appear to be errors and so represented real variation across the study area.

The environmental gradients indicated that TWINSPAN group III was associated with deeper, clearer water, lower sediment pH, phosphorus and nitrogen and less open habitats (1 = open, 5 = enclosed) than the other groups. Groups II and IV were separated on axis one indicating lower sediment iron and calcium and water conductivity in group II than group III.

Species ordination

As in the DCA diagram, the emergent and free-floating life-forms were not clearly separated as they were in the 2000 ordinations (Figure 2.24). The two bank-rooted, stoloniferous species *E. azurea* and *P. repens* were both at the far left of the diagram possibly indicating different habitat requirements of these species from the others. In fact, as *E. azurea* grew in abundance over most areas of the floodplain, it is possible that the other species points were indicating the unusual conditions in which *E. azurea* was less successful and other species had an opportunity to grow in the absence of its competition. The location of the *E. azurea* and *P. repens* species points indicated an association with high water conductivity and sediment nitrogen, phosphorus, calcium and iron which agrees with their position in the 2000 CCA.

CCA statistics

There were again high eigenvalues for this CCA at 0.511 for axis one and 0.443 for axis two. The first two axes represented the ordination well explaining 36.8% of the total variance in the species data and 46.0% of the total variance in the fitted values following regression on the environmental variables. The environmental data explained 80.0% of the species data. The canonical axes were not statistically significant and so the species data were not statistically significantly related to the environment.

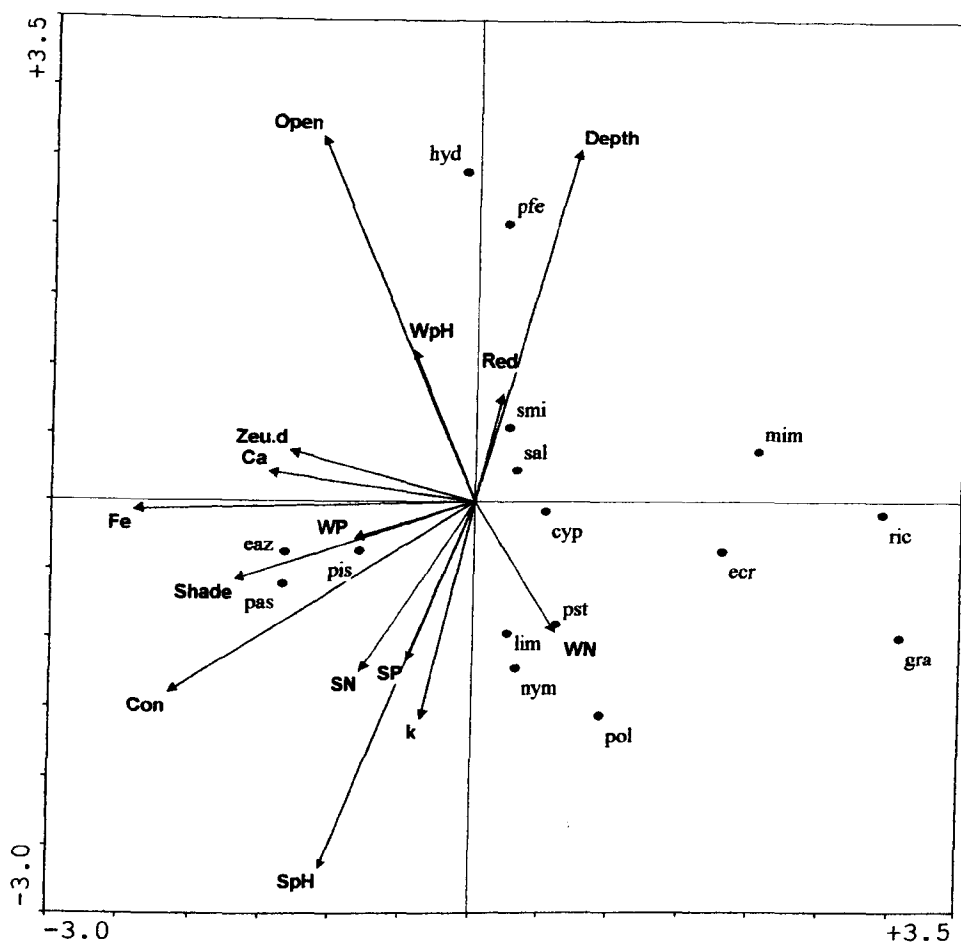


Figure 2.24 CCA species and environment biplot of 2001 data (COR2, ISL, PVF2, RPM2 supplementary). Axis 1 eigenvalue = 0.511, axis 2 eigenvalue = 0.443. Species codes are explained in Figure 2.22 and environmental variable codes in Figure 2.19.

2000-2001 CCA

This CCA illustrates all of the variation in the species data and environmental data measured over two years of data collection. Conditions differed between the two years with the second sampling period, 2001, following a spell of very low river levels. The variation is therefore associated with time effects as well as location within the floodplain.

The sample ordination for the 2000-2001 data set appears crowded due to the large number of sites and because there is one dominating trend across them (Figure 2.25). This separates some of the sites associated with the main channel of the Paraná due to their submerged community and the greater extension of the euphotic zone down to the sediment. These sites are not separated as strongly as in the DCA indicating that although the species composition may have been very different, the environmental conditions at the sites were not necessarily extreme in relation to some of the other sites. COR2 and ISL are clearly very different from all of the other sites, but the site points RPM and RPM2 are not

so distant from the other sites. Projection of the site points on to the Zeu/d gradient shows that several other sites had at least as good light penetration through the water column as RPM and RPM2 and so this is not necessarily the reason for the absence of submerged plants. The submerged species were mainly found in the fast-flowing Paraná or in waterbodies connected to it, such as Canal Cortado (COR2) and Ressaco do Pau Veio (PVF2), which might experience flow-related disturbance as a result. This water flow disturbance may be an important factor in preventing the growth of more robust, competitive species so that submerged plants are able to grow when there is sufficient light and less competition from larger plants. There may also be increased availability of the propagules of submerged plant species in habitats connected to the Paraná channel due to the proliferation of these species in the shallow, lentic environments of upstream reservoirs (Thomaz *et al.* 2004).

The species ordination shows that the submerged species were low on the sediment nitrogen and phosphorus and water phosphorus gradients (Figure 2.26). The floating and emergent species were mixed in the diagram. *E. azurea* appeared to be favoured by high sediment nitrogen, phosphorus, iron and calcium and water phosphorus.

Zeu/d, water depth and sediment nitrogen were the best single explanatory variables of species assemblage but sediment phosphorus was more important than sediment nitrogen when the variables were combined. There were a few extreme values in the environmental data (*e.g.*, high shade score at EDB, high *k* at GER, high sediment iron at LGA) but these did not appear to be errors. None of the variables had very high variance inflation factors (1.8-5.9), indicating that each was making some unique contribution to the regression.

The eigenvalue for axis one was 0.523 and for axis two was 0.238 and so axis one in particular was explaining the species data well. The two illustrated axes accounted for 15.9% of the total variance in the species data and 48.3% of the variance in the fitted values. Overall, the environmental data explained 32.9% of the total variance in the species data. The species data were not statistically significantly related to the environment.

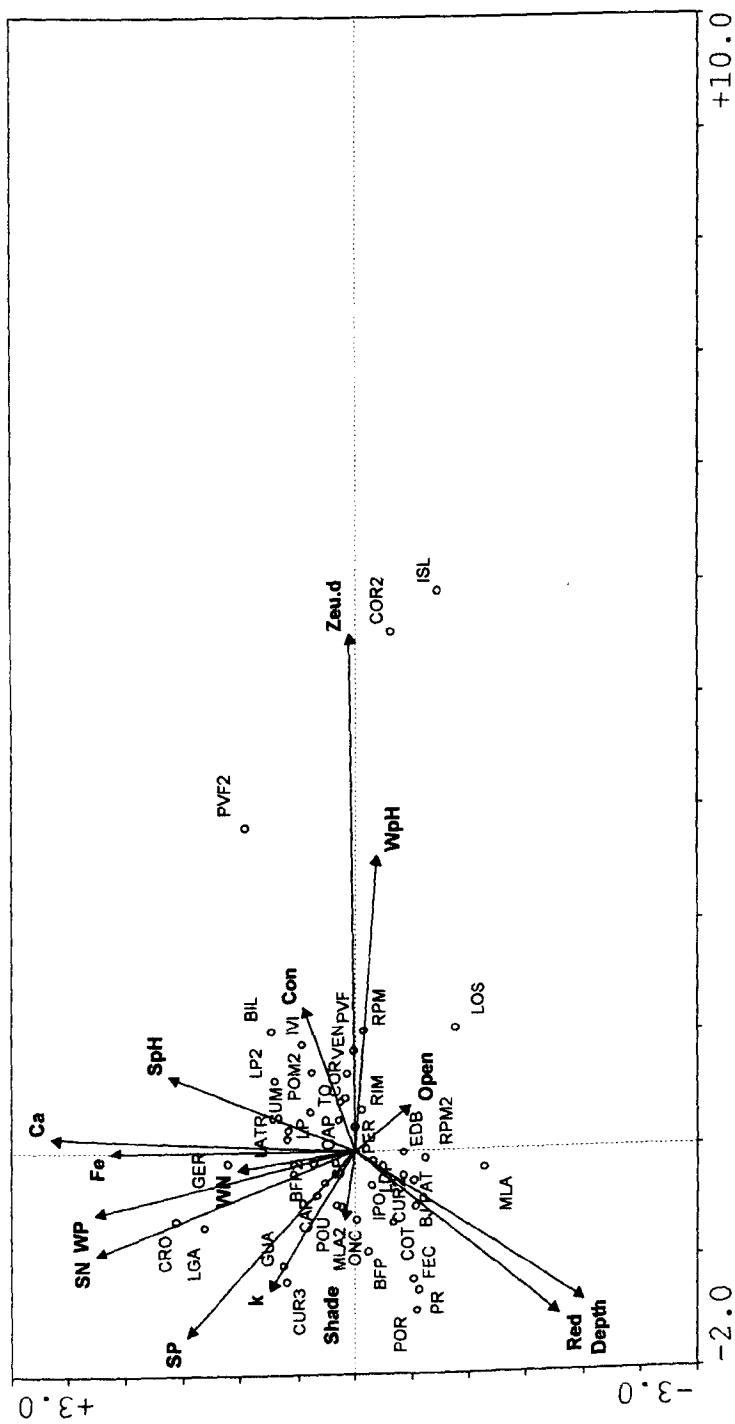


Figure 2.25 CCA site and environment biplot of 2000–2001 data. Axis 1 eigenvalue = 0.523, axis 2 eigenvalue = 0.238. Site codes are explained in Table 2.1 and environmental variable codes in Figure 2.19.

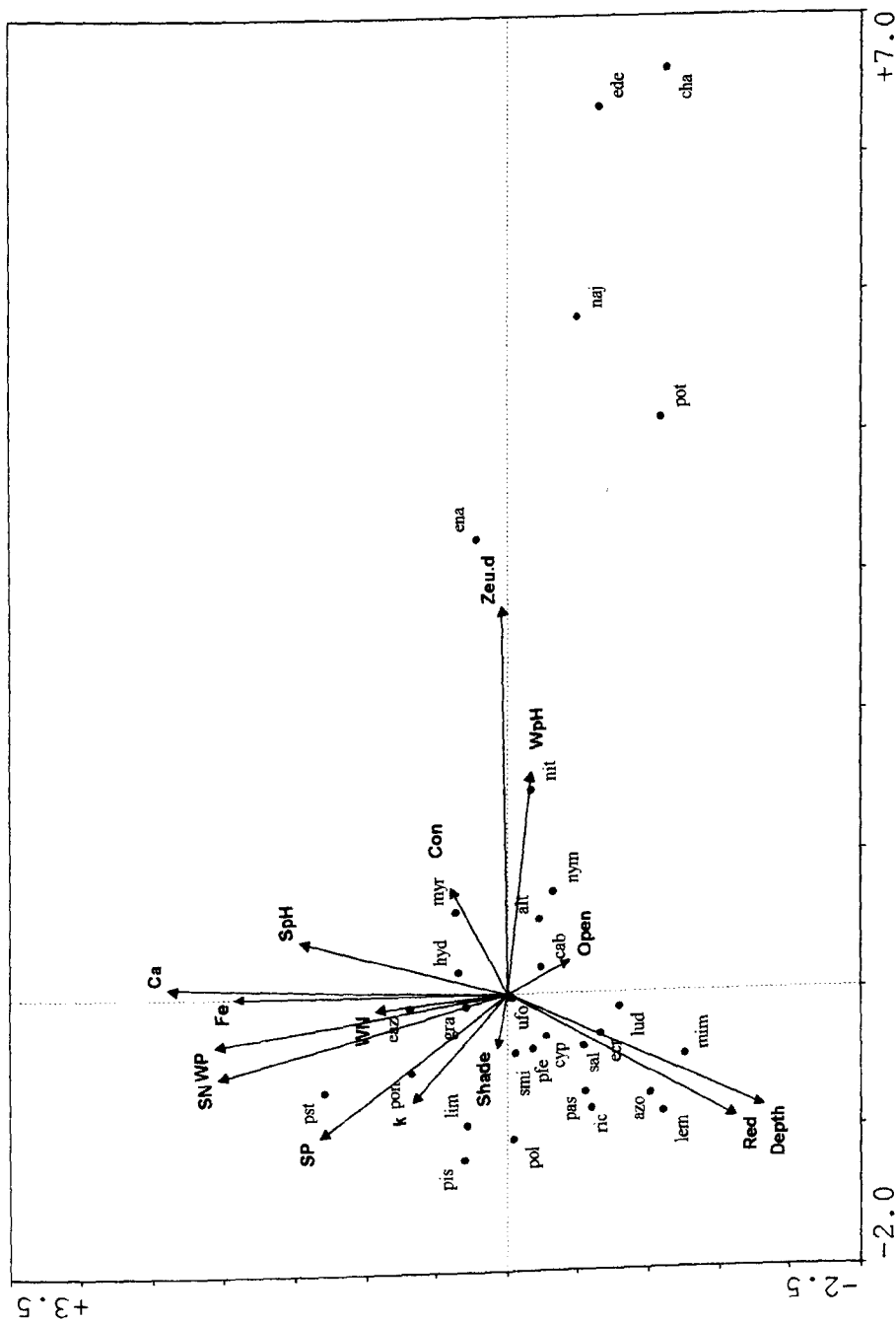


Figure 2.26 CCA species and environment biplot of 2000-2001 data. Axis 1 eigenvalue = 0.523, axis 2 eigenvalue = 0.238. Environmental variable codes are explained in Figure 2.19. azo *Azolla filiculoides*; alt *Alternanthera*; cab *Cabomba* sp.; cha *Chara* sp.; cyp *Cyperaceae*; eaz *Eichhornia azurea*; ecr *Eichhornia crassipes*; ede *Egeria densa*; ena *Egeria najas*; gra *Poaceae*; hyd *Hydrocotyle ranunculoides*; lem *Lemnaceae*; lim *Limnobium laevigatum*; lud *Ludwigia* sp.; mim *Mimosa pigra*; myr *Myriophyllum aquaticum*; naj *Najas* sp.; nit *Nitella* sp.; nym *Nymphaea amazonum*; pas *Paspalum repens*; pis *Pistia stratiotes*; pfe *Polygonum ferrugineum*; pol *Polygonum* sp.; pon *Pontederia cordata*; pot *Potamogeton pusillus*; pst *Polygonum stelligerum*; ric *Ricciocarpus natans*; sal *Salvinia* sp.; smi *Salvinia minima*; utr *Utricularia foliosa*.

2.4.4 Correlation and regression analysis of aquatic survey data:

Investigating relationships between environmental, collective vegetation and dominant species trait variables

2000

Table 2.27 shows a number of statistically significant Pearson product moment correlation coefficients between environmental, collective vegetation and dominant species trait variables at aquatic sites sampled in 2000. Table 2.28 shows the statistically significant regression relationships, which satisfied the assumptions of the linear regression model, between pairs of vegetation and environmental variables.

Table 2.27 Significant Pearson product moment correlation coefficients (r) between variables measured at aquatic sub-sites in 2000.

Variable 1	Variable 2	r	p
Spp	log _e Ca	-0.495	0.026
	Cover	+0.639	0.002
	log _e Stem	+0.446	0.049
log _e Biomass	log _e WN	+0.475	0.035
	Redox	+0.463	0.040
	SpH	-0.525	0.017
Height	log _e Z _{eu} /d	-0.461	0.047
	Height	+0.645	0.002
	SpH	-0.552	0.012
	log _e Z _{eu} /d	-0.710	0.001
	log _e Depth	+0.826	0.000
Cover	log _e Ca	-0.482	0.031
	log _e Stem	+0.640	0.002
	√ rwt	-0.477	0.033
	√ slen	-0.519	0.019
log _e Stem	SP	-0.446	0.049
	log _e Ca	-0.509	0.022
√ rwt	log _e WP	+0.505	0.023
√ slen	log _e SN	+0.581	0.007
	log _e Ca	+0.546	0.013
	log _e WP	+0.438	0.053
√ lwt	log _e WP	+0.449	0.047
	log _e SN	+0.539	0.014
	log _e Ca	+0.521	0.019

Correlation and regression analysis showed that species richness was significantly related to \log_e sediment calcium, percentage canopy cover and \log_e stem density. A positive linear relationship with percentage canopy cover explained the greatest amount of variation in species richness (40.8%). Alternatively, 24.5% of variation could be explained by a negative linear relationship with the only environmental predictor, \log_e sediment calcium. Combining the predictor variables in a multiple regression did not explain any further variation.

\log_e biomass could be predicted from \log_e water depth, \log_e water nitrogen, sediment redox potential, $\log_e Z_{eu}/d$ or canopy height. The best single predictor was \log_e water depth which explained 45.9% of variation in \log_e biomass in a quadratic relationship. Z_{eu}/d decreased linearly with \log_e biomass while each of the other variables increased linearly. Using multiple regression to combine the predictor variables did not increase the amount of variation explained by the model. The strong relationship between \log_e biomass and canopy height suggests that it may be possible to assess biomass by measuring canopy height instead of by the destructive method of cutting samples for weighing.

Canopy height could be predicted by sediment pH, \log_e water depth, $\log_e Z_{eu}/d$ or \log_e biomass. Canopy height was measured from the sediment to the top of the plant canopy and so for plants with floating parts, it was strongly related to water depth. The relationships of canopy height with water depth and Z_{eu}/d therefore were not considered because they resulted largely from the sampling method. The best predictor variable of canopy height was \log_e biomass (explaining 41.6% of variation), followed by sediment pH (explaining 30.4% of variation).

Percentage canopy cover increased linearly with species richness and stem density and decreased linearly with \log_e calcium, $\sqrt{\text{root weight}}$ and $\sqrt{\text{stem length}}$. The best single predictor of canopy cover was \log_e stem density (41.0% of variation explained) but this model was improved with the addition of a second predictor, species richness (Equation 2.1; 51.5% of variation explained). Square root stem length was the best trait predictor (26.9%) and \log_e sediment calcium the only environmental predictor (23.2%).

Equation 2.1

$$\text{Cover} = -68.300 + 16.990 \log_e \text{Stem} + 4.469 \text{Spp}$$

$$r = 0.752, \text{adjusted } r^2 = 0.515, p = 0.001, \text{S.e.} = 20.39.$$

\log_e stem density decreased linearly with \log_e sediment calcium and sediment phosphorus and increased linearly with species richness and canopy cover. The greatest amount of variation explained was by percentage canopy cover (41.0%), or if only environmental variables were considered, by \log_e sediment calcium (25.9%).

Table 2.28 Statistically significant regression equations relating vegetation and environment variables measured at aquatic sub-sites in 2000.

Relationship	r	r ²	p
Spp = 17.934 – 1.662 \log_e Ca	-0.495	0.245	0.026
Spp = 2.668 + 0.06315 Cover	+0.639	0.408	0.002
Spp = -3.44283 + 1.68941 \log_e Stem	+0.446	0.199	0.049
\log_e Bio = 6.068 + 1.235 \log_e Depth + 0.800 (\log_e Depth) ²	0.718	0.459 (adj)	0.0021
\log_e Bio = 1.591 + 0.774 \log_e WN	+0.475	0.226	0.035
\log_e Bio = 5.558 + 0.001663 Redox	+0.463	0.215	0.040
\log_e Bio = 6.19030 – 0.352219 \log_e z_{sed}/d	-0.462	0.213	0.047
\log_e Bio = 5.34566 + 0.787815 height	+0.645	0.416	0.002
Cover = 173.578 – 16.365 \log_e Ca	-0.482	0.232	0.031
Cover = 19.0774 + 6.47207 Spp	+0.640	0.409	0.002
Cover = -83.6859 + 24.5402 \log_e Stem	+0.640	0.410	0.002
Cover = 79.0143 – 11.4904 $\sqrt{\text{rwt}}$	-0.477	0.228	0.033
Cover = 94.0834 – 39.9726 $\sqrt{\text{slen}}$	-0.519	0.269	0.019
\log_e Stem = 9.008 – 0.451 \log_e Ca	-0.509	0.259	0.022
\log_e Stem = 6.67219 – 0.0785874 SP	-0.446	0.199	0.049
\log_e Stem = 5.14280 + 0.117893 Spp	+0.446	0.199	0.049
\log_e Stem = 4.88782 + 0.0167103 Cover	+0.640	0.410	0.002
Height = 4.10580 – 0.494857 SpH	-0.551	0.304	0.012
Height = 1.21595 + 1.26341 \log_e Depth + 0.491069 (\log_e Depth) ²	0.966	0.933 (adj)	0.000
Height = 1.20038 – 0.495330 \log_e z_{sed}/d	-0.710	0.504	0.001
Height = -2.24851 + 0.528017 \log_e Bio	+0.645	0.416	0.002
$\sqrt{\text{lar}}$ = -20.1906 + 10.5045 SP – 0.517614 SP ²	0.784	0.567 (adj)	0.000
$\sqrt{\text{rwt}}$ = -0.420122 + 0.693410 \log_e WP	+0.505	0.255	0.023
$\sqrt{\text{slen}}$ = -0.980205 + 0.249124 \log_e SN	+0.581	0.337	0.007
$\sqrt{\text{slen}}$ = -0.835002 + 0.240996 \log_e Ca	+0.547	0.299	0.013

Three of the dominant trait variables responded to the environmental variables. Sediment phosphorus explained 56.7% of the variation in $\sqrt{\text{leaf area}}$ in a quadratic relationship.

Square root root weight increased linearly with water phosphorus, which explained 25.5% of the variation. Square root stem length increased linearly with sediment nitrogen (33.7% of variation explained) and sediment calcium (29.9% of variation explained) but combining these variables did not increase the amount of variation in stem length explained because they were strongly inter-correlated themselves.

Summary

Sediment redox potential, pH, calcium and phosphorus and water depth, Z_{eu}/d and nitrogen may be important in determining collective vegetation structure. Species richness, percentage canopy cover and stem density (\log_e) all declined with sediment calcium (\log_e). Stem density (\log_e) also declined with sediment phosphorus. Biomass (\log_e) increased in more oxygenated sediments (higher redox potential) and when water was higher in nitrogen (\log_e). Biomass (\log_e) responded quadratically to depth (\log_e), declining at first in very shallow water and then increasing as water became deeper. Biomass (\log_e) and canopy height both decreased as the euphotic depth relative to the total water depth (\log_e Z_{eu}/d) increased. Biomass (\log_e) and canopy height were therefore greatest when the supply of PAR to the bottom of the waterbody was poor and lower as light availability increased permitting the growth of submerged plants.

The trait variables of the dominant species responded to sediment phosphorus, nitrogen and calcium and water phosphorus. Root weight ($\sqrt{}$) increased with water phosphorus (\log_e) and maximum stem length ($\sqrt{}$) increased with sediment nitrogen (\log_e) and calcium (\log_e). Leaf area ($\sqrt{}$) responded quadratically to sediment phosphorus (\log_e) increasing at first to a maximum and then decreasing.

Species richness increased with percentage canopy cover and with stem density (\log_e).

2001

Table 2.29 shows the statistically significant Pearson product moment correlation coefficients between pairs of vegetation and environmental variables. Table 2.30 shows the regression relationships, which fitted the data well and fulfilled the assumptions of linear regression, between pairs of variables.

Root weight of the dominant species and the leaf weight to root weight ratio were not considered in the analysis as there was a large number of missing values in the data. Residual analysis showed that some of the relationships did not fulfil the assumptions of the linear model and so were not considered any further. The relationships of canopy height with water depth and Z_{eu}/d were strongly influenced by the sampling method and so were rejected.

Table 2.29 Significant Pearson product moment correlation coefficients (r) between variables measured at aquatic sub-sites in 2001.

Variable 1	Variable 2	r	p
Spp	log _e Con	-0.475	0.022
	Fe	-0.466	0.025
	log _e Height	+0.575	0.004
	Cover	+0.560	0.007
	√ Biomass	+0.420	0.046
√ Biomass	log _e Con	-0.476	0.022
	SpH	-0.419	0.046
	log _e Height	+0.472	0.023
log _e Height	log _e Depth	+0.696	0.000
	log _e WpH	-0.557	0.006
	log _e Con	-0.585	0.003
	log _e z _{eu} /d	-0.612	0.002
	log _e lwt	+0.536	0.010
log _e Stem	log _e twt	+0.616	0.002
	Cover	+0.628	0.002
	log _e lwt	-0.631	0.003
	log _e slen	-0.446	0.056
	log _e rem	-0.592	0.006
Cover	log _e twt	-0.715	<0.001
	slen	-0.465	0.039
	log _e rem	-0.596	0.004
	Open	+0.442	0.039
	√ leaf area	log _e WP	-0.479
Shade		+0.478	0.024
log _e lwt	log _e WpH	-0.453	0.034
log _e twt	log _e WpH	-0.525	0.012
slen	Shade	+0.559	0.008
log _e rem	Shade	+0.428	0.047

Species richness increased linearly with log_e canopy height, percentage canopy cover and √ biomass and decreased linearly with log_e water conductivity and sediment iron content. Log_e water conductivity was the best environmental predictor explaining 22.5% of the variation in species richness while log_e canopy height was the best overall predictor explaining 33% of the variation. A model including both percentage canopy cover and canopy height as predictor variables explained the greatest amount of variation in species richness (42.2%; Equation 2.2).

Equation 2.2

$$\text{Spp} = 2.215 + 0.041 \text{ Cover} + 0.884 \log_e \text{ Height}$$

$$r = 0.690, \text{ adjusted } r^2 = 0.422, \text{ S.e.} = 1.67, p = 0.002.$$

Square root biomass increased linearly with \log_e water conductivity (after deletion of one outlier) and decreased linearly with \log_e canopy height. There were quadratic relationships between $\sqrt{\text{biomass}}$ and percentage canopy cover and $\sqrt{\text{biomass}}$ and species richness. \log_e water conductivity was the best predictor of $\sqrt{\text{biomass}}$ explaining 40.2% of the variation. Combining the significant predictor variables in a multiple regression did not increase the amount of variation explained.

\log_e canopy height increased linearly with species richness and with \log_e total weight of the dominant species and decreased linearly with \log_e water pH and \log_e conductivity and \log_e leaf weight of the dominant species. The best environmental predictor of \log_e canopy height was \log_e water conductivity, which explained 34.2% of the variation, while the best predictor overall was \log_e total weight of the dominant species which explained 37.9% of the variation. Multiple regression analysis showed that combining \log_e total plant weight and \log_e conductivity increased the amount of variation in canopy height explained to 55.8% (Equation 2.3).

Equation 2.3

$$\log_e \text{ Height} = 2.024 + 0.283 \log_e \text{ twt} - 0.951 \log_e \text{ Con}$$

$$r = 0.775, \text{ adjusted } r^2 = 0.558, \text{ S.e.} = 0.748, p < 0.001.$$

Canopy cover did not respond significantly to any of the environmental variables but increased linearly with \log_e canopy height (after deletion of four outlying points) and species richness, decreased linearly with stem length of the dominant species and was quadratically related to \log_e stem density. \log_e canopy height was the best single predictor of canopy cover. No further variation was explained by combining the predictor variables.

\log_e stem density also did not respond to the environmental variables but increased linearly with percentage canopy cover and responded quadratically to \log_e leaf weight and \log_e remainder weight. The best single predictor was \log_e total leaf weight of the dominant species which explained 56.5% of the variation in \log_e stem density. The significant

relationship of \log_e stem density with \log_e total weight of the dominant species was rejected because it appeared to depend upon the strong influence of outliers.

Square root leaf area of the dominant species decreased linearly with \log_e water phosphorus which explained 23% of the variation. Pearson correlation coefficients showed that \log_e leaf weight and \log_e total plant weight decreased linearly with \log_e water pH but these relationships depended on two outlying points and so were rejected. There were no further relationships between the traits of the dominant species and the environmental variables.

Table 2.30 Statistically significant regression equations relating vegetation and environment variables measured at aquatic sub-sites in 2001.

Regression relationship	r	r ²	p
Spp = 10.747 – 1.871 \log_e Con	-0.474	0.225	0.022
Spp = 5.682 – 0.000031 Fe	-0.466	0.217	0.025
Spp = 4.996 + 1.171 \log_e Height	+0.574	0.330	0.014
Spp = 1.743 + 0.049 Cover	+0.559	0.313	0.007
Spp = 2.113 + 0.097 $\sqrt{\text{Biomass}}$	+0.506	0.256	0.016
$\sqrt{\text{Biomass}}$ = 67.517 – 13.166 \log_e Con	-0.634	0.402	0.002
$\sqrt{\text{Biomass}}$ = 27.124 + 5.933 \log_e Height	+0.472	0.223	0.023
$\sqrt{\text{Biomass}}$ = -18.239 + 1.300 Cover – 0.009 Cover ²	0.549	0.227(adj.)	0.033
$\sqrt{\text{Biomass}}$ = -3.591 + 12.482 Spp – 1.148 Spp ²	0.610	0.309	0.010
\log_e Height = 14.073 – 7.752 \log_e WpH	-0.503	0.311	0.006
\log_e Height = 3.274 – 1.132 \log_e Con	-0.585	0.342	0.011
\log_e Height = -1.880 + 0.282 Spp	+0.574	0.330	0.004
\log_e Height = -1.162 – 0.320 \log_e lwt	-0.536	0.287	0.010
\log_e Height = -1.460 + 0.335 \log_e twt	+0.616	0.379	0.002
Cover = 68.728 + 23.859 \log_e Height	+0.709	0.502	0.001
Cover = -249.389 + 91.068 \log_e Stem – 6.175 (\log_e Stem) ²	0.676	0.397(adj.)	0.004
Cover = 36.691 + 6.415 Spp	+0.559	0.313	0.007
Cover = 78.891 – 0.176 Slen	-0.466	0.217	0.039
\log_e Stem = 4.167 + 0.025 Cover	+0.628	0.395	0.002
\log_e Stem = 6.051 – 0.690 \log_e lwt + 0.145 (\log_e lwt) ²	0.782	0.565(adj.)	0.000
\log_e Stem = 6.593 – 0.959 (\log_e rem+1) + 0.154 (\log_e rem+1) ²	0.657	0.364(adj.)	0.008
$\sqrt{\text{lar}}$ = 65.387 – 9.150 \log_e WP	-0.480	0.230	0.024

Table 2.31 Spearman rank correlation coefficients (r) for SLA.

Variable 1	Variable 2	r	p
SLA	WpH	+0.515	0.014
	Height	-0.483	0.023
	Stem	+0.624	0.003

Calculation of Spearman rank correlation coefficients showed that SLA of the dominant species increased with water pH and stem density and decreased with canopy height (Table 2.31). Sediment redox potential and site openness were not significantly correlated with any of the vegetation variables.

Summary

In the 2001 data set, species richness, biomass ($\sqrt{}$) and canopy height (\log_e) all decreased as water conductivity (\log_e) increased. Canopy height (\log_e) also decreased with water pH (\log_e). Total leaf area per plant of the dominant species ($\sqrt{}$) decreased with water phosphorus (\log_e) while SLA increased with water pH (\log_e).

Species richness increased with canopy height (\log_e), percentage canopy cover and biomass ($\sqrt{}$).

2000-2001

Table 2.32 lists the significant Pearson product-moment correlation coefficients between vegetation and environmental variables. Table 2.33 shows the regression equations describing these relationships which satisfied the assumptions of linear regression and fitted the data well.

Table 2.32 Significant Pearson product-moment correlation coefficients (*r*) between vegetation variables and environmental variables recorded at aquatic sub-sites during 2000 and 2001.

Variable 1	Variable 2	<i>r</i>	<i>p</i>
Spp	log _e Depth	+0.313	0.041
	log _e Ca	-0.296	0.054
	√ Height	+0.524	<0.001
	Cover	+0.529	<0.001
	log _e Stem	+0.351	0.025
log _e Biomass	log _e Z _{eu} /d	-0.463	0.003
√ Height	log _e WpH	-0.363	0.017
	log _e Con	-0.297	0.053
	Cover	+0.373	0.015
Cover	log _e Stem	+0.612	<0.001
	√ slen	-0.514	0.001
log _e Stem	Open	+0.327	0.037
	√ slen	-0.412	0.009
√ slen	log _e SN	+0.395	0.010
	log _e Ca	+0.420	0.006

Species richness increased linearly with log_e water depth, √ canopy height, percentage canopy cover and log_e stem density and decreased linearly with log_e sediment calcium (which was correlated with other nutrients). Log_e water depth was the best environmental predictor explaining 9.8% of the variation in species richness while percentage canopy cover was the best overall predictor and explained 27.9% of the variation. R² (adjusted) was increased to 0.383 by combining percentage canopy cover, √ canopy height and log_e sediment calcium by multiple regression (Equation 2.4).

Equation 2.4

$$\text{Spp} = 6.596 + 0.02852 \text{ Cover} + 2.654 \sqrt{\text{Height}} - 0.765 \log_e \text{Ca}$$

$r = 0.655$, adjusted $r^2 = 0.383$, $p < 0.001$.

Log_e biomass (three particularly low biomass sites deleted to normalise data) decreased linearly as the proportion of the water column able to support photosynthesis (log_e Z_{eu}/d) increased. Sites with high light availability throughout the water column tended to support submerged species, which are usually lightweight, instead of floating ones, which are usually bulky and heavy. Log_e biomass (three outlying sites deleted) also responded

quadratically to \log_e water nitrogen content although $\log_e Z_{eu}/d$ was the better predictor. Combining these predictor variables by multiple regression did not increase the amount of variation in biomass explained.

Square root canopy height decreased linearly with conductivity and increased linearly with species richness and percentage canopy cover. There was a significant correlation between $\sqrt{\text{canopy height}}$ and \log_e water pH but in the regression analysis the residuals were not normally distributed so this relationship was rejected. \log_e water conductivity was therefore the only environmental predictor of $\sqrt{\text{canopy height}}$. It explained 8.8% of the variation. Species richness was the best overall predictor and explained 27.5% of the variation in $\sqrt{\text{canopy height}}$. An equation including both \log_e water conductivity and species richness as predictor variables increased the amount of variation explained to 30.4% (Equation 2.5).

Equation 2.5

$$\sqrt{\text{Height}} = 1.279 + 0.0681 \text{ Spp} - 0.209 \log_e \text{Con}$$

$$r = 0.581, \text{ adjusted } r^2 = 0.304, p < 0.001.$$

Percentage canopy cover was not significantly related to any of the environmental variables but increased linearly with $\sqrt{\text{canopy height}}$, species richness and \log_e stem density and decreased linearly with $\sqrt{\text{stem length}}$ of the dominant species. \log_e stem density was the best single predictor explaining 37.5% of the variation in percentage canopy cover but this was increased to 57.8% when \log_e stem density, $\sqrt{\text{canopy height}}$ and $\sqrt{\text{stem length}}$ of the dominant species were combined in a multiple regression (Equation 2.6).

Equation 2.6

$$\text{Cover} = -30.019 + 15.386 \log_e \text{Stem} + 26.025 \sqrt{\text{Height}} - 23.644 \sqrt{\text{slen}}$$

$$r = 0.782, \text{ adjusted } r^2 = 0.578, \text{ S.e.} = 17.51, p < 0.001.$$

\log_e stem density decreased linearly with $\sqrt{\text{stem length}}$ of the dominant species, increased linearly with species richness and percentage canopy cover and responded quadratically to $\sqrt{\text{canopy height}}$. Stem density increased as sites became less open (openness score

increased). Percentage canopy cover was the best single predictor explaining 37.5% of the variation. Combining the predictor variables did not increase r^2 .

Square root stem length of the dominant species increased linearly with \log_e sediment nitrogen content and \log_e sediment calcium content. \log_e sediment calcium explained slightly more variation ($r^2 = 17.6\%$) and combining the two variables in a multiple regression did not increase this any further.

Table 2.33 Statistically significant regression equations relating vegetation and environment variables measured at aquatic sub-sites in 2000-2001.

Relationship	r	r ²	p
Spp = $5.92178 + 0.938982 \log_e \text{ Depth}$	+0.313	0.098	0.041
Spp = $10.8131 - 0.804790 \log_e \text{ Ca}$	-0.295	0.087	0.054
Spp = $1.915 + 3.88 \sqrt{\text{Height}}$	+0.524	0.275	<0.001
Spp = $1.963 + 0.05425 \text{ Cover}$	+0.529	0.279	<0.001
Spp = $-1.014 + 1.107 \log_e \text{ Stem}$	+0.351	0.123	0.025
$\log_e \text{ Biomass} = 6.38153 - 0.378375 \log_e Z_{\text{eu}}/d$	-0.464	0.215	0.003
$\log_e \text{ Biomass} = 32.0690 - 9.295 \log_e \text{ WN} + 0.825896 (\log_e \text{ WN})^2$	0.382	0.100(adj.)	0.054
$\sqrt{\text{Height}} = 1.62900 - 0.207689 \log_e \text{ Con}$	-0.297	0.088	0.053
$\sqrt{\text{Height}} = 0.493159 + 0.0708214 \text{ Spp}$	+0.524	0.275	<0.001
$\sqrt{\text{Height}} = 0.557974 + 0.0051407 \text{ Cover}$	+0.373	0.139	0.015
Cover = $95.346 - 38.474 \sqrt{\text{slen}}$	-0.514	0.265	0.001
Cover = $39.1881 + 27.0036 \sqrt{\text{Height}}$	+0.373	0.139	0.015
Cover = $35.2795 + 5.15178 \text{ Spp}$	+0.528	0.279	<0.001
Cover = $-46.9313 + 18.8866 \log_e \text{ Stem}$	+0.612	0.375	<0.001
$\log_e \text{ Stem} = 6.714 - 0.972 \sqrt{\text{slen}}$	-0.412	0.170	0.009
$\log_e \text{ Stem} = 7.44975 - 3.74775 \sqrt{\text{Height}} + 1.89751 \text{ Height}$	0.436	0.147(adj.)	0.018
$\log_e \text{ Stem} = 5.26385 + 0.111059 \text{ Spp}$	+0.351	0.123	0.025
$\log_e \text{ Stem} = 4.60395 + 0.0198353 \text{ Cover}$	+0.612	0.375	<0.001
$\sqrt{\text{slen}} = -0.0004506 + 0.116568 \log_e \text{ SN}$	+0.395	0.156	0.010
$\sqrt{\text{slen}} = -0.208482 + 0.151353 \log_e \text{ Ca}$	+0.420	0.176	0.006

Table 2.34 shows Spearman rank correlation coefficients calculated for relationships with variables which were not normally distributed. Canopy height increased with the redox potential of the sediment and decreased with sediment pH. Biomass and species richness both decreased with sediment pH. Specific leaf area of the dominant species increased with water pH and decreased with sediment phosphorus, nitrogen and calcium. Leaves became thinner in more alkaline water and thicker when sediment phosphorus, nitrogen

and calcium increased. The ratio of leaf weight to root weight of the dominant species increased with water conductivity.

Table 2.34 Significant Spearman rank correlation coefficients (r) for non-normal environmental and vegetation variables recorded at aquatic sub-sites during 2000 and 2001.

Variable 1	Variable 2	r	p
Height	Redox	+0.374	0.015
	SpH	-0.361	0.017
Biomass	SpH	-0.417	0.005
Spp	SpH	-0.412	0.006
SLA	WpH	+0.308	0.047
	SP	-0.305	0.050
	SN	-0.369	0.016
	Ca	-0.324	0.036
lw/rw	Con	+0.374	0.022

Summary

Collective vegetation structure responded to several environmental variables. Species richness increased with water depth (\log_e) and decreased as sediment calcium (\log_e) and sediment pH increased. Biomass (\log_e) decreased as Z_{eu}/d (\log_e) and sediment pH increased and responded quadratically to water nitrogen (\log_e). Canopy height ($\sqrt{}$) decreased as water conductivity (\log_e) and sediment pH increased, and increased with sediment redox potential. Stem density increased with the openness score so stem density was higher when sites were more sheltered by surrounding vegetation than when they were open.

The maximum stem length of the dominant species increased as sediment nitrogen (\log_e) and calcium (\log_e) increased.

Species richness increased with canopy height ($\sqrt{}$), percentage canopy cover and stem density (\log_e).

2.4.5 Testing the outcomes of the analyses

Testing 2000-2001 TWINSpan and ordination results with the 2002 data set

The aquatic sites sampled in 2002 can be assigned to the TWINSpan groups derived from the 2000-2001 data according to their species assemblages.

The species compositions at CAR2, CUR4, TIA, IVI3 and JAC suggest that they belong to the vegetation type represented by TWINSpan group I. Sites in this group tended to have a mixed community of floating species, very abundant *Salvinia* sp., increased importance of *Eichhornia crassipes* and reduced dominance of *Eichhornia azurea*.

JAC was typical of this group with a high abundance of *E. crassipes*, *S. minima* and *Salvinia* sp. but not *E. azurea*. CUR4 had abundant *E. azurea* but also had four other free-floating species including *Salvinia minima* and *Salvinia* sp. CAR2 had no *E. azurea* or *E. crassipes* but had *Paspalum repens* and four free-floating species including *S. minima* and *Salvinia* sp. (although *Myriophyllum aquaticum* in its emergent form was dominant). TIA had very abundant *E. crassipes* and no *E. azurea* but no other free-floating species. Both *E. azurea* and *E. crassipes* were absent from ZEM and in low abundance at IVI3. These sites were placed in this group because they had abundant *Polygonum* species which mainly occurred at sites in group I.

It was expected that the variables that had distinguished 2000-2001 TWINSpan groups I, II and III would not differ significantly between each group and the 2002 sites assigned to that group. Water depth, conductivity and pH, sediment phosphorus and nitrogen, species richness, canopy height, biomass, percentage canopy cover, stem density, total leaf weight, specific leaf area, total root weight, total plant weight and maximum stem length did not differ significantly between 2000-2001 group I and the 2002 sites assigned to this group (Table 2.35). Z_{eu}/d did differ significantly between 2000-2001 group I and the 2002 sites assigned to this group. Mean Z_{eu}/d was higher in the 2002 sites than the group I sites, which were associated with particularly low Z_{eu}/d , and intermediate between mean Z_{eu}/d in groups II and III. The large data set showed that in general, Z_{eu}/d was important in determining vegetation composition. However, the 2002 results show that other factors have an effect so that although the sites considered to belong to TWINSpan group I had high Z_{eu}/d , they did not have the expected species composition previously associated with this state.

Table 2.35 Mean and standard error (or median* – canopy cover and total root weight) of environmental, collective vegetation and dominant species trait variables in 2000-2001 TWINSPAN group I and 2002 sites assigned to TWINSPAN group I. The p-value indicates the significance of difference between the means determined by a t-test or between the medians* determined by a Kruskal-Wallis test.

Variable	2000-2001	S.e.	2002	S.e.	p
	Group I		Group I		
Water depth m	1.11	0.19	0.67	0.28	0.193
Zeu/d	1.27	0.28	4.10	0.97	0.001
Water pH	6.55	0.11	6.52	0.21	0.885
Water conductivity μScm^{-1}	35.61	5.72	29.67	3.52	0.755
Sediment total ext. P mgkg^{-1}	18.04	3.51	20.92	5.59	0.956
Sediment TKN mgkg^{-1}	2650	853	2768	1135	0.705
Canopy height m	1.36	0.20	1.10	0.42	0.395
*Canopy cover %	84.44		79.72		0.702
Stem density m^{-2}	557	111	330	123	0.078
Biomass gm^{-2}	1056	181	865	192	0.877
Species richness per site	6.95	0.61	6.83	0.98	0.926
Maximum stem length m	0.66	0.14	1.02	0.27	0.212
Total leaf dry weight g per plant	11.87	4.13	7.15	2.85	0.849
Specific leaf area cm^2g^{-1}	320	107	139.9	44.1	0.212
*Total root dry weight g per plant	3.40		0.65		0.122
Remainder dry weight g per plant	8.22	4.06	7.81	2.94	0.253
Total plant dry weight g per plant	27.00	8.38	16.06	5.47	0.954

2000-2001 TWINSPAN group II consisted of sites where *E. azurea* was abundant, *Nymphaea amazonum* was often present and free-floating species and *Polygonum* species were rare. LP3, BFP3, CID, FRA, MAN and PDG fitted best with this group.

LP3 fitted the group well with abundant *E. azurea* and moderately abundant *N. amazonum*. BFP3 and FRA were strongly dominated by *E. azurea* and had only one other species each, but no *N. amazonum*. CID had no *E. azurea* and MAN had only very low abundance, but *N. amazonum* was respectively in moderate and very high abundance at these two sites. PDG was dominated by *E. azurea* with three other species present, each at very low abundance.

Comparisons between the characteristics of 2000-2001 TWINSPAN groups and the 2002 sites assigned to these groups are shown in Table 2.36. The mean values of the environmental variables measured across the 2000-2001 TWINSPAN group II sites did not differ from those measured at the 2002 sites assigned to group II. Biomass, species

richness and percentage canopy cover were also similar. However, total stem density and leaf weight and total weight of the dominant species did differ between the 2000-2001 group and the 2002 group. Group II had the lowest stem density of the 2000-2001 TWINSpan groups, and stem density was lower still in 2002 group II. The 2002 sites therefore fitted the pattern of stem density relative to the other groups. Similarly, total leaf dry weight and total plant dry weight of the dominant species were found to be highest of the three groups in 2000-2001 group II and were higher still in 2002 group II. The mean values of these variables in 2002 group II therefore agreed with the patterns observed in 2000-2001 group II.

Table 2.36 Mean and standard error of environmental, collective vegetation and dominant species trait variables in 2000-2001 TWINSpan group II and 2002 sites assigned to TWINSpan group II. The p-value indicates the significance of difference between the means determined by t-tests.

Variable	2000-2001 Group II	S.e.	2002 Group II	S.e.	p
Water depth m	0.47	0.07	0.65	0.15	0.261
Z_{av}/d	2.29	0.56	2.51	0.60	0.801
Water pH	6.64	7.47	6.75	0.19	0.581
Water conductivity μScm^{-1}	45.68	7.05	35.33	4.98	0.178
Sediment total ext. P mgkg^{-1}	16.93	2.16	14.75	5.43	0.390
Sediment TKN mgkg^{-1}	2834	582	3658	1143	0.558
Canopy height m	0.64	0.07	0.81	0.18	0.319
Canopy cover %	47.49	5.46	65.28	5.71	0.098
Stem density m^{-2}	285.2	56.9	125.9	52.0	0.016
Biomass gm^{-2}	433.3	96.3	418	135	0.941
Species richness per site	4.32	0.48	3.00	0.45	0.160
Maximum stem length m	1.18	0.12	1.40	0.28	0.387
Total leaf dry weight g per plant	16.04	3.9	46.2	13	0.019
Specific leaf area cm^2g^{-1}	244.6	84.9	117.2	31	0.658
Total root dry weight g per plant	5.28	1.34	9.54	2.69	0.087
Remainder dry weight g per plant	22.49	5.22	45.9	20.1	0.524
Total plant dry weight g per plant	43.27	9.13	101.6	33.7	0.039

2000-2001 TWINSpan group III consisted of sites where only submerged species were present. RPM3 was the only site to satisfy this condition in the 2002 data set. RPM is compared with 2000-2001 TWINSpan group III in Table 2.37. Like RPM and RPM2, it was located in the main channel of the Paraná River but not in the same place. In common with the group III sites, RPM3 had particularly high Z_{av}/d and water pH and particularly low sediment nitrogen and phosphorus. Water depth was similar to the mean water depth

of group III while water conductivity was lower. Trait measurements of the dominant species at this site, *Potamogeton pusillus*, were not available but this species and other morphologically similar submerged rooted species were typical of group III sites. Biomass and species richness were very low at RPM3 and group III was associated with low values for both of these variables. The environmental conditions and the vegetation characteristics of RPM3 therefore closely resembled those of the sites in 2000-2001 TWINSPAN group III.

Table 2.37 Mean and standard error of environmental, collective vegetation and dominant species trait variables in 2000-2001 TWINSPAN group III and the 2002 site RPM3 assigned to this group.

Variable	2000-2001 Group III	S.e.	RPM3
Water depth m	0.43	0.26	0.49
Zcu/d	8.96	2.92	10.79
Water pH	7.47	0.29	8.49
Water conductivity μScm^{-1}	60.0	12.6	38
Sediment total ext. P mgkg^{-1}	4.74	1.43	1.07
Sediment TKN mgkg^{-1}	676	435	80
Biomass gm^{-2}	117.8	35.3	1.97
Species richness per site	2.6	0.93	3

The positioning of the 2002 sites on the ordination diagram agreed well with the TWINSPAN groups to which they were assigned (Figure 2.27). The sites Baía floodplain (BFP1-3), Ressaco do Leopoldo (LP1-3) and Curutuba Channel (COT, CUR3, CUR4) were each sampled in 2000, 2001 and 2002. BFP2 and BFP3 have moved slightly upwards on axis two away from BFP. LP3 has moved down axis two from LP and LP2 and slightly to the right. CUR3 and CUR4 have moved up from COT and slightly to the right towards the TWINSPAN group II sites. The movement of points representing sites that were sampled more than once shows variation in species assemblage at these sites between the years. This suggests year on year variation in environmental conditions. Despite the upstream damming of the river, there are still general flood-pulse related patterns that can be expected in floodplain conditions due to seasonal and hydrological variations. but there is variation within these patterns. Winter is the season of low river levels but in 2001 the water levels were particularly low in the floodplain due to low rainfall as well as retention of water in the upstream reservoirs. Water depth in itself has been shown to be very important in determining species composition. Wind action is also more likely to cause resuspension of sediment in shallow water bodies resulting in reduced water transparency.

Lagoons which would usually remain connected to the Paraná, Baía or Ivinheima Rivers, even during the low water season, became disconnected and therefore diverged in environmental conditions. The vegetation could be expected to respond to these environmental changes leading to variation in species data between years. However, the movement in site points was not great, and the samples collected from the same sites in different years remained in the same TWINSpan groups indicating that one vegetation community was not replaced with another between years.

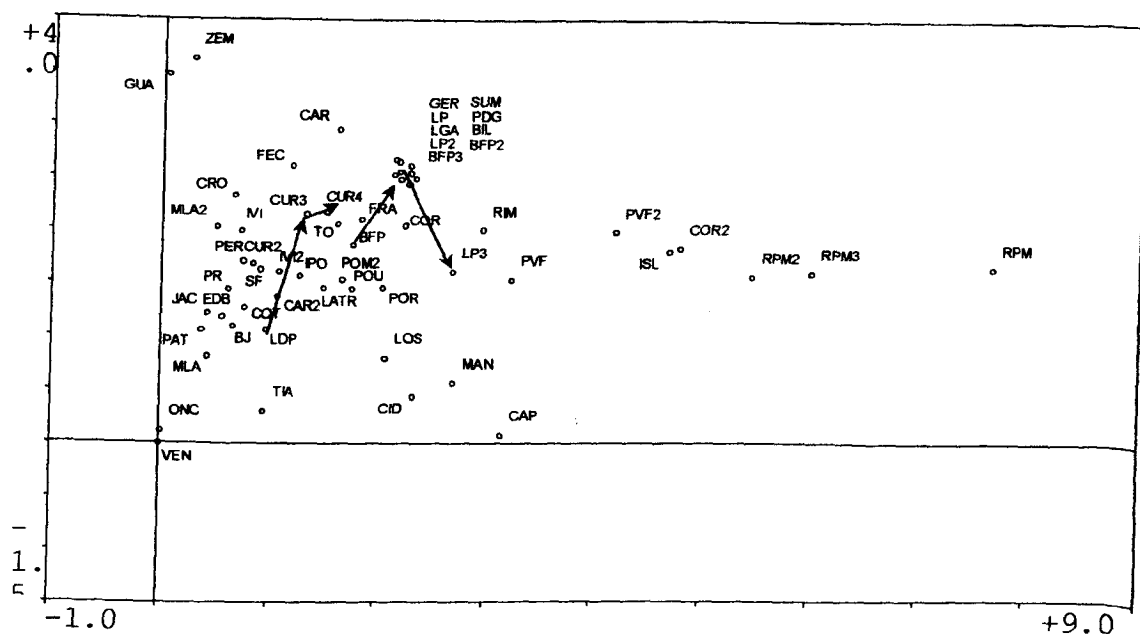


Figure 2.27 2000-2002 DCA site ordination. Axis 1 eigenvalue = 0.830, axis 2 eigenvalue = 0.416. Site codes are explained in Table 2.1. Arrows show migration of sites sampled in all three years, Baía floodplain (BFP1-3), Ressaco do Leopoldo (LP1-3) and Curutuba Channel (COT, CUR3, CUR4).

The 2002 data set was found to agree with the results of analysis of the 2000-2001 data set. The vegetation communities and associated environmental gradients detected by cluster and ordination analysis proved to be robust. The testing procedure indicated that the vegetation and environmental patterns detected during analysis of the 2000-2001 data set were realistic and could be observed in independent sites.

Testing the regression equations derived from the 2000-2001 data set

The relationships tested were:

$$\text{Spp} = 6.596 + 0.02852 \text{ Cover} + 2.654 \sqrt{\text{Height}} - 0.765 \log_e \text{Ca}$$

$$\sqrt{\text{Height}} = 1.279 + 0.0681 \text{ Spp} - 0.209 \log_e \text{Con}$$

$$\text{Cover} = -30.019 + 15.386 \log_e \text{Stem} + 26.025 \sqrt{\text{Height}} - 23.644 \sqrt{\text{slen}}$$

$$\log_e \text{Biomass} = 6.38153 - 0.378375 \log_e z_{\text{eu}}/d$$

$$\sqrt{\text{slen}} = -0.208482 + 0.151353 \log_e \text{Ca}$$

The values of species richness, canopy height, canopy cover, biomass and stem length of the dominant species at 2002 sampling sites predicted using regression equations derived from the 2000-2001 data set were not significantly correlated ($p > 0.05$) with the actual measured values (Table 2.38).

This indicated that the 2002 data did not closely follow the regression lines calculated from the 2000-2001 data. However, each equation explained only a portion of the variation in the response variable (17.6% to 57.8%) and so it was expected that the predicted and actual results would not always agree. Table 2.38 shows the predicted and actual values of each variable. It can be seen that predicted species richness was within two species of the actual value at seven out of twelve sites. The regression equation used to predict species richness had an r^2 value of 38%. The regression relationship for the prediction of canopy height explained 30% of the variation in the original data. The predicted values were within 20cm (maximum height = 1.73m) of the actual values at three out of twelve sites. The predictive equation for canopy cover explained 58% of the variation and cover was predicted within 10% of the actual value at one third of the sites. Biomass was predicted within 100g (maximum biomass = 1535g) at one quarter of sites by a regression equation expected to explain 22% of the variation in biomass. The stem length of the dominant species was predicted within 10cm of the actual value (maximum = 2.33m) at two out of twelve sites. The regression equation explained 18% of the variation in the original data. The 2002 data did not confirm the general applicability of the regression equations but this would have been difficult because of the small proportion of variation in the response variables for which they accounted.

Table 2.38 Values of species richness (Spp), canopy height (Height), % canopy cover (Cover), Biomass and stem length of the dominant species (Slen) measured at 2002 sites paired with values predicted from the regression equations developed from the 2000-2001 data set. (Spp predicted from cover, $\sqrt{\text{height}}$ and $\log_e \text{Ca}$, Height predicted from Spp and $\log_e \text{con}$, Cover predicted from $\log_e \text{Stem}$, $\sqrt{\text{Height}}$ and $\sqrt{\text{Slen}}$, Biomass predicted from $\log_e \text{Zeu/d}$ and Slen predicted from $\log_e \text{Ca}$).

Site	2002 Spp	Pred. Spp	2002 Height	Pred. Height	2002 Cover	Pred. Cover	2002 Biomass	Pred. Biomass	2002 Slen	Pred. Slen
LP3	3	5.16	1.04	0.42	51.67	32.78	245.94	349.49	1.37	0.82
CAR2	11	4.82	0.26	1.73	70.56	64.62	834.40	277.64	0.73	0.66
ZEM	5	5.22	0.85	0.78	53.89	48.27	927.20	291.91	1.41	0.73
CUR4	7	5.86	0.87	1.23	63.33	49.08	325.24	430.12	1.51	0.62
BFP3	2	6.69	1.14	0.40	70.56	16.83	477.10	547.92	2.33	0.54
CID	3	3.42	0.20	0.59	44.44	37.75	52.00	449.89	0.63	0.82
TIA	7	5.83	0.42	1.32	88.89	46.01	371.42	382.88	0.14	0.63
FRA	2	5.91	1.33	0.50	77.22	35.15	739.08	493.44	2.00	0.95
IVI2	4	10.57	3.11	0.68	90.00	41.21	1535.10	533.04	1.84	0.20
RPM3	3	-	-	0.52	-	-	1.97	240.57	-	0.21
JAC	7	6.10	1.10	0.95	93.33	80.91	1199.08	350.57	0.50	0.95
MAN	5	6.08	0.59	0.75	78.33	62.18	131.26	330.21	0.65	0.55
PDG	3	5.15	0.53	0.77	69.44	23.85	863.44	511.92	1.44	0.73

2.4.6 Variation in morphological traits of *Eichhornia azurea* and *Eichhornia crassipes*

TWINSPAN analysis of the 1999 species data revealed three major vegetation types occurring within aquatic habitats of the floodplain. The characteristics of these groups are outlined in Section 2.4.2 and compared and discussed in detail by Murphy *et al.* (2003).

Group A consisted of nine sites and was indicated by abundant *Salvinia* sp., moderately abundant *Cyperus diffusis* and the presence of *Limnobium laevigatum*. Group B was indicated by a low abundance of *Cyperus diffusis*, a high abundance of *Salvinia* sp. and the absence of *Limnobium laevigatum*. This was the largest group, with 30 sites. Group C was made up of six sites and was indicated by the absence of *Salvinia* sp.

In all groups, *Eichhornia azurea* was a strong dominant, present at most stations at high abundance. Group A consisted of sites with water that tended to be deeper and clearer than in the other groups, with low conductivity, alkalinity and phosphate concentration. Sediment calcium, iron and phosphorus were low, but total nitrogen was high compared to other sites. This suggests that the group represents habitats with deep water and good light availability but in general, poorer availability of nutrients. *E. azurea* was a dominant

component of the vegetation, while high abundances of free-floating species were also characteristic of this group, possibly facilitated by the provision of sheltered habitats between *E. azurea* stems. *E. crassipes* was present in moderate abundance at all but one site in this group. In the larger group B, sites had very variable water and sediment properties and therefore did not tend to differ significantly from other groups. *E. azurea* was in high abundance, again with frequent floating species, but the emergent *Polygonum* species and *Panicum prionitis* were absent. *E. crassipes* was present at just over half the sites in this group, mainly at low abundance. Group C sites were shallow with generally cloudier water than the other sites. Water and sediments were nutrient-rich. *Nymphaea amazonum* in combination with submerged species such as *Myriophyllum aquaticum* and *Cabomba* sp. were commonly present in sites of this group while the abundance of *E. azurea* was conspicuously reduced, although it still tended to be the most frequent species at each site. *E. crassipes* was absent.

The range of trait measurements recorded for *E. azurea* and *E. crassipes* are indicated in Table 2.39 and Table 2.40 respectively. All variables measured showed wide ranges, representing a large sample of the variation present in the floodplain.

Table 2.39 Median, minimum and maximum measurements of *Eichhornia azurea* traits per 15 node sample in 1999.

Trait	Median	Minimum	Maximum
Total leaf dry weight (g)	52.16	6.74	218.20
Total leaf area (cm ²)	3123	228	14514
Specific leaf area (cm ² g ⁻¹)	66.47	13.24	155.70
Total root dry weight (g)	21.54	2.90	119.70
Leaf weight / root weight	2.14	0.29	33.34
Remainder dry weight (g)	98.05	8.90	350.30
Total plant dry weight (g)	181.2	25.6	538.5
Maximum stem length (m)	2.27	0.94	3.60

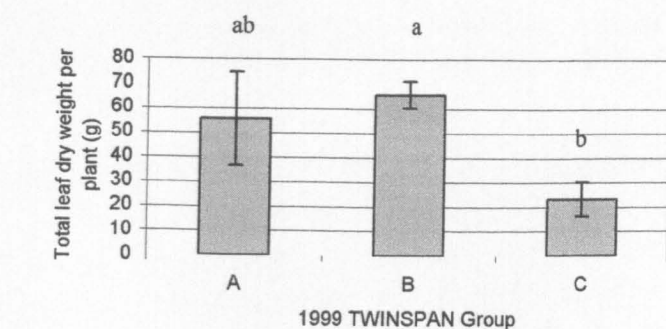
Total leaf weight ($p = 0.021$), leaf thickness (SLA $p < 0.001$) and the ratio of leaf weight to root weight ($p = 0.008$) of *E. azurea* were significantly greater in group B (means = 65.79g, 48.88cm²/g, 1.54 respectively) than group C (means = 23.35g, 106.9cm²/g, 1.25 respectively) (Figure 2.28 a-c). Leaves were also significantly thicker in group A (mean = 47.33cm²/g) than group C. *E. azurea* therefore had greater abundance, greater frequency of dominance and more developed leaves in group B, the most common vegetation type identified, than in group C. In group C, conditions were more favourable for the growth of

submerged species than in the other groups in which emergent or floating life-forms dominated. Shallow water, although it tended to be cloudy, allowed sufficient light to penetrate for underwater photosynthesis so that the aerial leaves of *E. azurea* may not have created as much of a survival advantage as in other habitats. When competing with species with similar requirements for water surface area or bank rooting positions, *E. azurea* tended to be extremely successful. However, when it occurred where the environment permitted the growth of species with different growth strategies, it could not maintain the same degree of dominance over the other species. The species clearly has wide environmental tolerances but showed a reduction in its success when growing near the limits of these tolerances.

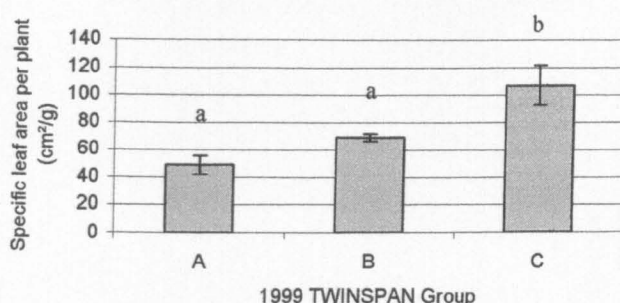
Table 2.40 Median, minimum and maximum measurements of *Eichhornia crassipes* traits per individual in 1999.

Trait	Median	Minimum	Maximum
Total leaf dry weight (g)	12.37	1.60	40.20
Total leaf area (cm ²)	1221	99	5506
Specific leaf area (cm ² g ⁻¹)	98.7	52.2	630.1
Total root dry weight (g)	4.20	0.11	30.50
Leaf weight / root weight	2.07	0.32	90.97
Remainder dry weight (g)	2.50	0.01	9.00
Total plant dry weight (g)	24.10	1.81	79.70
Maximum stem length (m)	0.420	0.15	1.61

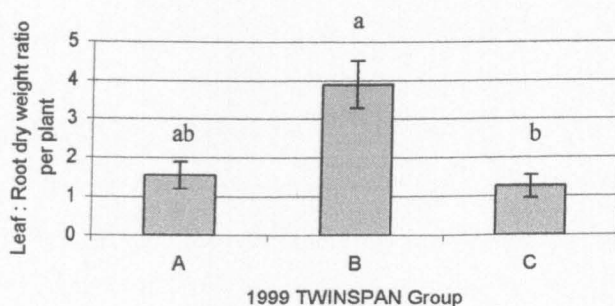
Although much less abundant than *E. azurea*, *E. crassipes* is also important due to its widespread presence over most areas of the floodplain. It is also usually the dominant species when *E. azurea* is not. *E. crassipes* plants had significantly greater total leaf dry weight ($p = 0.009$), total leaf area ($p = 0.018$) and total plant dry weight ($p = 0.008$) in group A (means = 25.17g, 2704cm², 42.64g respectively) than in group B (means = 4.49g, 484cm², 8.64g respectively). No other measured traits differed significantly between the two groups. The greater success of *E. crassipes* in group A coincides with lower *E. azurea* abundance compared to group B and so could be due to the greater suitability of the sites for the free-floating rather than the bank-rooted species. The generally lower nutrient status of sediments at group A sites may have prevented *E. azurea* from maximising its growth, thus permitting greater development of *E. crassipes*. The deeper water of group A sites may also have favoured the free-floating form of many of the species in this group.



a



b



c

Figure 2.28 a-c Means and standard errors of three morphological traits of *Eichhornia azurea* which differed significantly between TWINSpan vegetation groups A, B and C. Groups without a letter in common were significantly different.

Significant Pearson correlation coefficients for relationships between *E. azurea* trait variables and environmental variables (1999-2001) are given in Table 2.41. The results of the correlation analysis show that \log_e leaf : root weight ratio increased linearly with sediment iron and \log_e calcium (Table 2.41). When sediment was rich in iron or calcium, investment in roots was low in relation to leaves. A possible explanation for this is that high levels of reduced iron (Fe^{2+}) in anoxic sediment can produce toxic conditions for roots and restrict growth (Snowden & Wheeler 1993).

Table 2.41 Pearson product-moment correlation coefficients (r) and probability (p) for linear relationships between *Eichhornia azurea* trait variables and environment variables (1999-2001).

<i>E. azurea</i> trait variable	Environmental variable	r	p
log _e leaf weight / root weight	sediment Fe	+0.222	0.039
log _e leaf weight / root weight	log _e sediment Ca	+0.271	0.011
√ total leaf dry weight	log _e water depth	+0.250	0.018
log _e total leaf area	log _e water depth	+0.320	0.002
maximum stem length	log _e water depth	+0.278	0.008
√ remainder dry weight	log _e water depth	+0.288	0.006
√ total plant dry weight	log _e water depth	+0.293	0.005
log _e total leaf area	log _e k	-0.225	0.036
maximum stem length	log _e k	-0.352	0.001
√ remainder dry weight	log _e k	-0.269	0.012
√ total plant dry weight	log _e k	-0.261	0.014

In this study, spatial variation in water depth was a very important factor influencing *E. azurea* traits. Total leaf weight, total leaf area, maximum stem length, total remainder weight and total plant weight all increased linearly with water depth (Table 2.41).

Individual *E. azurea* plants were therefore generally larger in deep water habitats. This could be an effect of reduced competition because plants with submerged growth forms may have been excluded from these habitats due to low light availability in deep water, while emergent species may not have been able to tolerate the depth of flooding. Such deep water habitats are suitable for floating species, but *E. azurea* has an advantage over these in being able to use the sediment as well as the water as a source of nutrients.

E. azurea growth was also increased at sites with higher water clarity. Total leaf area, maximum stem length, remainder weight and total plant weight all decreased with log_e k (Table 2.41). Good light availability is important for the initial establishment of this species because the seedling develops underwater. Although photosynthesis in the mature plant is not directly affected by water clarity, water clarity depends on phytoplankton concentration and suspended and dissolved substances which may in turn affect the growth of *E. azurea*.

In *E. crassipes*, log_e water depth was positively correlated with log_e total leaf dry weight ($r = 0.665$, $p = 0.007$) and total plant dry weight ($r = 0.520$, $p = 0.047$). Log_e remainder dry weight was negatively correlated with sediment phosphate concentration ($r = -0.554$, $p =$

0.032). In addition to the linear correlations, there were two quadratic relationships (Equations 2.7 and 2.8).

Equation 2.7

$$\text{Total root dry weight (g)} = 31.6168 - 0.0423861\text{Ca} + 1.48 \times 10^{-5} \text{Ca}^2$$

$$r = 0.558, \text{ adjusted } r^2 = 0.478, p = 0.011.$$

Equation 2.8

$$\text{Total plant dry weight (g)} = 33.2920 - 24.8630 (\log_e Z_{\text{eu}}/d) + 9.27379 (\log_e Z_{\text{eu}}/d)^2$$

$$r = 0.713, \text{ adjusted } r^2 = 0.419, p = 0.020.$$

E. crassipes total root weight initially declined with sediment calcium content, reached a minimum at approximately 1500mg/kg and then increased with increasing calcium. Total plant weight initially decreased with $\log_e Z_{\text{eu}}/d$ and then levelled off at higher values of $\log_e Z_{\text{eu}}/d$ before beginning to increase again.

The cubic relationship between total root weight and sediment calcium shows that total root weight was maximised either at low or high levels of calcium and minimised at intermediate levels. This could be explained if proportionally greater investment is made in roots when calcium is in short supply, in order to maximise uptake, than when levels are intermediate. High calcium levels may generally stimulate plant growth resulting in heavier roots again.

Total plant weight initially decreased with $\log_e Z_{\text{eu}}/d$ and then slightly increased again. Although *E. crassipes* does not rely on underwater photosynthesis, it might be affected by the influence of water clarity on other species. For example, clearer water would make a habitat more available to species which do photosynthesise underwater and might provide greater competition in these circumstances. $\log_e Z_{\text{eu}}/d$ was also correlated with sediment calcium which at intermediate levels was associated with increased root growth.

The strong positive relationship of leaf weight and total plant weight with water depth indicates a general advantage of deeper water to *E. crassipes*. Shallow water limits the volume of water available for root expansion. It could also encourage growth of emergent species or submerged-rooted species which might compete with *E. crassipes*.

The decrease in remainder weight with sediment phosphorus may be explained if high levels of phosphorus stimulate production of daughter plants resulting in a lower average stem weight per plant.

2.5 Discussion

In total, 31 taxa comprising spermatophytes, pteridophytes, charophytes and one bryophyte were recorded during the surveys of aquatic sub-sites. The growth forms of these plants consisted of: bottom-rooted with submerged foliage; unrooted submerged; bottom-rooted with floating leaves; bank-rooted with floating stems; free-floating; and emergent. So far 62 species have been recorded during on-going surveys of the floodplain near Porto Rico field station (Thomaz *et al.* 2004). This study aimed to describe the large amount of variation in vegetation and environmental factors occurring across the floodplain and so lagoons and channels were not surveyed exhaustively. However, the species encountered during the surveys certainly represented the most significant species (by abundance) in this part of the floodplain.

The diversity in environmental conditions recorded across the sampling sites helps to explain how the system can support such a wealth of species with varying requirements for growth. However, despite this diversity, a small number of species were found to dominate at the sampling sites. These were *E. azurea*, *E. crassipes* and *Salvinia* sp. The morphological plasticity of *E. azurea* and *E. crassipes* appeared to allow these two species to adapt to different growth conditions and to integrate with or dominate more than one community type.

2.5.1 Vegetation communities

Individual years

During 2000, sites associated with the Paraná and Baía Rivers were sampled. A large proportion of these sites were temporary, seasonal lagoons. This type of habitat was rare in 2001 due to low rainfall and water retention in the reservoirs upstream, which produced a very low flood that year and prevented the lagoons from being refilled. Instead, permanently flooded sites associated with the Paraná, Baía and Ivinheima rivers were sampled. It was therefore expected that some differences between TWINSPLAN vegetation communities might be found in the two data sets. However, comparable communities were found. In 2000, groupings based on species composition corresponded with

associations with different rivers so that the Baía sites were principally in group I, the Paraná sites in group III while group II included sites from both rivers. Similarly, in 2001, group I consisted of only main channel Paraná sites while group II was mainly Baía sites, group III consisted of Baía and Ivinheima sites and group IV had sites from all three rivers. This broad association of vegetation communities with specific rivers is due to the differing physical and chemical properties of the Paraná, Baía and Ivinheima. These differences were shown in 2000 by contrasting water depth and underwater light attenuation while in 2001 the different vegetation types were associated with different levels of water electrical conductivity and pH. As the groups were not differentiated by the same variables over the two years, it is difficult to compare them based on environmental features. However, there are similarities between the 2000 and 2001 TWINSpan groups in the vegetation itself. Group II from 2000 and group IV from 2001 are relatively species-poor groups strongly dominated by *E. azurea*. In both groups, the vegetation is short with low stem density and large, heavy dominants. 2000 group I and 2001 group III illustrate an alternative role which *E. azurea* can play as a less dominant component of a floating community with high diversity and evenness. In these types of communities, *E. azurea* may provide shelter from flow disturbance for smaller, free-floating plants which might otherwise be washed away. These two communities in which *E. azurea* is a significant component show that this species may suppress species richness when it is very successful and therefore highly dominant, while it may be involved in stimulating increased species richness by providing habitats for free-floating species when it is less dominant.

2000 group III and 2001 group II are similar because *E. azurea* is not a very important component and both include *Nymphaea amazonum*. However, in 2000 these sites were associated with the Paraná while in 2001 they were associated with the Baía. The 2001 group I sites appear to correspond with the only main channel Paraná site sampled in 2000, RPM, which supported only submerged rooted species.

2000-2001

During 2000 and 2001, a representative set of floodplain waterbodies was sampled from the range of habitats which vary from year to year and in factors such as flow characteristics and proximity to the three rivers present in this stretch of the floodplain. Some similarities were found between vegetation communities derived from data from individual years while differences were attributed to these sources of variation. Analysis of the two-year data set has identified broad vegetation communities which show some agreement with a data set of comparable size collected in 1999. The data suggest that a

mixed, high diversity, high biomass community in which *E. azurea* co-exists with a selection of abundant floating and emergent species is associated with deep, semi-lotic to lotic waterbodies with low water conductivity and nitrogen-rich sediments. In addition, there is a more species-poor community type in which *E. azurea* strongly dominates the vegetation. This is associated with shallow, slower-flowing water with high conductivity and nitrogen and phosphorus-rich sediment. A possible sub-community, indicated by *N. amazonum* growing together with submerged species, was separated in analysis of the 1999 and 2000 data. This is associated with shallow, turbid, high conductivity water and iron-, calcium- and phosphorus-rich sediment. A final community, which was found only in sites within or very close to the main channel of the Paraná, consists entirely of low biomass, submerged plants rooted in well-illuminated nitrogen- and phosphorus-poor sediment.

Testing of the 2000-2001 TWINSpan output with a new data set collected in 2002 showed that the vegetation communities identified were realistic and persisted over time.

The association of these vegetation types with particular environmental properties can suggest likely shifts in community if the factors suspected to control them begin to change. For example, in years of low water levels during summer, temporary lagoons are not filled and so one habitat-type is removed from the system for that period. In addition, the nutrient cycling role of the flood is lost if terrestrial vegetation is not drowned, decomposed and returned to the waterbodies. Temporary lagoons are important in supporting vegetation group II which is associated with shallow, nutrient-rich habitats and so the frequency and distribution of this community is likely to be affected by low water. Reduced water depth and flow velocity caused by river regulation could potentially, in some floodplain locations, lead to a shift from the higher biomass, more diverse *E. azurea* community (associated with deeper, faster-flowing water) to the lower biomass, less diverse *E. azurea* community (associated with shallower, slower-flowing water).

The large data set illustrates the importance of floodplain heterogeneity in supporting at least three distinct aquatic vegetation types. Water depth, pH, conductivity and clarity and sediment nitrogen and phosphorus appear to strongly influence broad vegetation types while more subtle variation may be expected to result in sub-communities. These factors are sensitive to anthropogenic impacts such as river regulation and nutrient-rich pollutant discharges which can therefore be expected to influence plant species composition, diversity and biomass.

2.5.2 Floodplain gradients

The results of the indirect and direct gradient analyses showed that most of the environmental variables measured during the study appeared to play some part in influencing species assemblage. Across the two-year data set, variation in species assemblages was associated with water depth, Z_{eu}/d , sediment nitrogen (best three explanatory variables in CCA of 2000-2001 data), water pH, water conductivity, water nitrogen, water phosphorus, the underwater light extinction coefficient, sediment nitrogen, sediment phosphorus, sediment calcium and sediment pH. Gradients of species turnover were correlated with gradients of biomass, species richness, canopy cover, canopy height and the dominant species traits stem length, total leaf weight, total leaf area, total remainder weight and total plant weight. These gradients in species assemblage, collective vegetation structure, dominant species traits and the environment are linked because the environmental conditions at any particular site will favour a vegetation community with suitable adaptations to those conditions, resulting in the occurrence of species assemblages with the structural (and underlying physiological) properties necessary for success. The community is further determined by the biotic interactions between the set of species physiologically equipped for growth at any particular site.

For example, shallow water habitats with high water conductivity, water pH and sediment pH and a high proportion of the water column sufficiently illuminated for photosynthesis supported submerged species. These were low biomass, low canopy cover and low diversity short communities of small, lightweight individuals. Thin leaves are necessary to allow rapid diffusion of gases in and out of submerged plants while a lightweight, unligified structure permits them to anchor at the bottom of fast-flowing water where large, competitive species are absent. Their low investment in structural tissue means that they have low nutrient requirements, allowing them to survive in low nutrient environments. Their physiology is thus related to their physiognomy and their physiognomy to the physical features of their habitat.

In contrast, free-floating species tended to be associated with deep water habitats where water and sediment pH and water conductivity tended to be low. Light intensity at the bottom of such deep waterbodies was probably insufficient for photosynthesis of submerged species while the physiological challenge of underwater growth for emergent species up to the surface was probably too great. However, for free-floating plants, the water surface provided a large area for colonisation where there was plenty of room for root expansion allowing efficient nutrient uptake, and high surface light intensity available

for capture by aerial leaves. These communities were species rich with high biomass and canopy cover and well-developed root systems. These structural features are suitable for maximising photosynthesis and nutrient uptake and therefore competitive ability in the presence of additional species.

The dominant species in the floodplain, *E. azurea*, belongs to neither of these groups but has a life-form that allows it to take advantage of many resources simultaneously. It was almost ubiquitous, varying slightly in abundance and in morphology. High sediment nitrogen, phosphorus, calcium and iron and water phosphorus were particularly favourable for this species which has large leaves and high biomass making it a competitive species. Analysis of the 2000 data suggested emergent species preferences for shallow water which was more turbid than in the habitats where submerged species occurred. Emergent species were also associated with more oxygenated, nutrient-rich sediment and nutrient-rich water which provided the less stressful conditions necessary for them to reach their often large size.

2.5.3 Predictive relationships

During analysis of the two-year data set (2000-2001), species richness was found to be related to the environmental variables water depth, sediment calcium and sediment pH, biomass to Z_{cu}/d , water nitrogen and sediment pH, and canopy height to water conductivity, sediment redox potential and sediment pH. Future human impacts on the floodplain which may result in changes to any of these variables can be expected to have an effect upon vegetation structure. Therefore, these may be appropriate environmental factors for monitoring the threat to floodplain vegetation from environmental change.

Species richness, canopy height and canopy cover were each best predicted by more than one variable, including other collective vegetation variables and dominant trait variables. Species richness increased with canopy height, canopy cover and stem density. Short, low cover and low stem density vegetation at species-poor sites suggests stressful growth conditions. The number of species adapted to conditions occurring at such sites can therefore be expected to be low due to the special adaptations required for survival. In conditions more favourable for the development of tall, denser vegetation, the number of species potentially able to colonise a habitat can be expected to be greater. In this case, the number of species increased linearly with canopy height, canopy cover and stem density. In the humpback model of species diversity in relation to productivity (Grime 1973), the large number of species physiologically able to grow in a productive environment leads to

plant competition. This biotic factor is expected to limit the number of successful species to the most competitive ones, leading to a subsequent decline in species diversity. No decline was observed in the 2000-2001 data with species richness being maximised at sites with greatest canopy height, canopy cover and stem density. It is likely that the vegetation assemblages present in the Paraná floodplain do not represent the wide variation in biomass which would be necessary to demonstrate the humpback model of species diversity in relation to production.

2.5.4 Variation in morphological traits of *Eichhornia azurea* and *Eichhornia crassipes*

Comparison of *E. azurea* traits between vegetation communities has shown that this species is likely to be responding to spatial variation in environmental and plant interaction conditions by showing plasticity in its leaf morphology. This was detected as variation in total leaf weight, specific leaf area and the leaf to root weight ratio. *E. crassipes* also showed variation in leaf morphology (leaf area, leaf biomass and total biomass) providing further evidence for leaf adaptations to variations in conditions experienced by the macrophyte communities occurring within the river floodplain. Correlation and regression analysis of individual pairwise relationships between dominant plant traits and environmental variables showed weak but highly significant relationships and it is likely that many factors interact to determine the success of the *Eichhornia* species. The allocation of resources to roots relative to leaves was influenced by sediment iron and calcium content. The responses of five different trait variables indicated that *E. azurea* reacted to increased water depth with an overall increase in size.

E. azurea biomass per unit area has also been shown to vary with the annual fluctuations in water level in the floodplain (Bini 1996). The greatest amount of living material was found during the period of March to June when water levels were at their highest. During July to November, total *E. azurea* phytomass reached a maximum, but a greater proportion was comprised of dead material.

Variation in root biomass with seasonal variation in a floodplain lake of the Rio Mogi-Guaçu, located at a similar latitude to the Paraná floodplain, has been shown by Camargo & Esteves (1996). *E. azurea* root biomass reached its maximum in September when water total Kjeldahl nitrogen and total phosphorus were lowest, and its minimum in January when total Kjeldahl nitrogen and total phosphorus were highest. During the low temperatures, water levels and nutrient conditions of September, rhizomes and leaves were

at their lightest. The nitrogen and phosphorus contents of rhizomes and leaves reflected the concentrations of these nutrients in the water (Camargo & Esteves 1996). The results showed that seasonal variation in morphology and tissue nutrient content of *E. azurea* were closely tied to the influence of the annual flood pulse.

Both *Eichhornia* species are clearly capable of adapting to natural changes in habitat as well as to those likely to be underway due to river regulation. However, water clarity and depth and nutrient cycling are important factors in structuring populations of *E. azurea* and *E. crassipes* and so spatial and temporal changes in their growth can be anticipated. The analysis of *Eichhornia* morphology in relation to growth conditions across sites where it is not necessarily dominant would provide a fuller picture of its environmental tolerances.

2.6 Conclusions

- 31 plant taxa of a variety of life-forms were recorded during three sampling seasons from aquatic habitats in the Porto Rico stretch of the Paraná River floodplain.
- The most abundant species throughout the sampling area were *Eichhornia azurea*, *Salvinia* sp. (*S. herzogii* and *S. auriculata*) and *Eichhornia crassipes*. These were also most frequently the dominant species at individual sites.
- The aquatic vegetation of the Paraná River floodplain in the vicinity of Porto Rico can be classified into three major community types.
- Community types differ in species assemblage, associated environmental conditions, collective vegetation structure and morphological traits of the dominant species.
- Species assemblages across the sampling sites varied with gradients of water depth, Z_{eu}/d , sediment nitrogen, water pH, water conductivity, water nitrogen, water phosphorus, water turbidity, sediment nitrogen, sediment phosphorus, sediment calcium and sediment pH.
- Gradients of species turnover were correlated with gradients of biomass, species richness, canopy cover, canopy height and the dominant species traits stem length, total leaf weight, total leaf area, total remainder weight and total plant weight.

- Species richness, biomass and canopy height could be predicted from a combination of environmental variables and other collective vegetation variables.
- Variation in species richness was partially explained by water depth, sediment calcium, canopy height, canopy cover and stem density. A predictive equation of species richness by canopy cover, canopy height and sediment calcium accounted for 40% of the variation. Variation in biomass was partially explained by Z_{eu}/d and water nitrogen. Canopy height increased with water conductivity. 30% of the variation in canopy height was explained by prediction from species richness and water conductivity. (Results from 2000-2001 data set).
- The stem length of the dominant species was also related to environmental variables, increasing with sediment nitrogen and calcium.
- Testing of vegetation groupings and vegetation-environment relationships derived from the 2000-2001 data set with a small test data set collected in 2002 showed the results of the analyses to be robust and generally applicable within the location and sampling period of this study.
- Two of the most frequently dominant species, *Eichhornia azurea* and *Eichhornia crassipes*, responded to variation in habitat conditions and vegetation community type with variation in morphological traits.
- The results of this chapter provide information on the environmental and vegetation factors that influence the aquatic vegetation communities of the floodplain. The identified vegetation-environment relationships provide targets for monitoring the status of the floodplain habitats and are of value for the prediction of possible consequences of future anthropogenic impacts on the floodplain.

3 Bank and floodplain vegetation communities of the Paraná River floodplain

3.1 Aims

- To describe the vegetation adjacent to waterbodies, and extending into the floodplain, by its species assemblages, by its physical structure and by the morphological traits of the dominant species.
- To identify relationships between these vegetation characteristics and environmental gradients in the floodplain.
- To test these relationships using a test data set including new independent sampling sites and repeat sites.

3.2 Introduction

The Paraná floodplain encompasses a range of habitats along a continuum from open water through wetlands to terrestrial areas. The aquatic vegetation described and discussed in Chapter Two occupies a relatively small area of the floodplain. Overall, the floodplain is dominated, by area, by the vegetation of the “aquatic terrestrial transition zone” (ATTZ; Junk, Bayley & Sparks 1989). Chapter Three uses some of the methods introduced in Chapter Two to investigate patterns in the vegetation and environmental characteristics of the banks and shores of waterbodies (B sub-sites) and of adjacent floodplain areas (C sub-sites) which make up the ATTZ.

In addition to the threat from river regulation, these areas of the floodplain have in the past been exploited for grazing cattle and growing crops, resulting in the clearance of forested areas and destruction of natural vegetation by livestock. Cattle still graze in some areas and fires started in order to clear vegetation are also a common source of disturbance. A knowledge of the types of vegetation currently found in the floodplain, and the factors which influence them, may contribute to the effective management of the area and allow it to be used in a sustainable way for cattle ranching, subsistence farming and tourism.

In Chapter Three, TWINSpan analysis is used to identify broad vegetation communities at bank and floodplain sub-sites. The vegetation and environmental characteristics of the

sub-sites are compared between these communities. Correlation and regression analysis are used to investigate relationships between environmental, collective vegetation and dominant species trait variables.

3.3 Methods

3.3.1 *Field and laboratory*

Field surveys were conducted as described in Chapter Two, section 2.3.1. In this chapter, the data collected from the bank and floodplain sub-sites are analysed and discussed. Vegetation and environment surveys were carried out at bank and/or floodplain habitats adjacent to the waterbodies listed in Table 2.1 (locations illustrated in Figure 2.5). In 2000, both a bank area (B or B2 sub-sites) and a floodplain area (C sub-sites) were surveyed at most sites. In 2001, where the exceptionally low river level had exposed a new bank habitat, this was considered an additional sub-site (B1 sub-sites) and was also surveyed giving four different sub-sites at some locations (Figure 3.1).



Figure 3.1 Shore of Lagoa do Bile sampled in 2001, showing the temporary shore in the foreground (B1 sub-site), the more vegetated area which would form the shore during normal springtime water levels (B2 sub-site) and the slightly more elevated, wooded levee (C sub-site) in the background.

The same set of collective vegetation and dominant species trait variables was measured at bank and floodplain sites as at aquatic sites in 2000, but as it was very difficult to remove intact root systems from the drier, harder soil, the root weight of the dominant species was not measured in 2001 and 2002. An example of a biomass sample taken from a C sub-site, avoiding loose dead plant material, is shown in Figure 3.2. The environmental variables measured were soil pH, soil total Kjeldahl nitrogen, soil ADAS extractable phosphorus, soil total calcium and soil total iron. Soil was prepared for pH measurement by mixing a sample in a beaker with distilled water to produce a paste in which the pH probe could be submerged. Grazing, shade and openness scores were assessed as before, and additionally, the approximate distance of the sub-site from the associated waterbody and its approximate elevation above the surface of this waterbody were measured.



Figure 3.2 Biomass sample removed from a 0.25m x 0.25m square at Pau Veio Forest (PVF2) sub-site C, November 2000.

3.3.2 Data analysis

As in Chapter Two, species lists and summary statistics for the environmental, collective vegetation and dominant species trait variables were tabulated for each year.

TWINSpan analysis was conducted separately for B sub-sites and C sub-sites using the methods described in Chapter Two, Section 2.3.2. In 2000 and 2001, plant samples were identified as far as possible using books and keys. Samples which could not be identified

were categorised as creepers, woody plants, herbaceous dicotyledonous plants, ferns, saplings or seedlings. Species assemblage data were entered into TWINSpan as the abundance of a family, genus, species or category at each sub-site. In 2002, Kazue Kawakita Kita MSc., a plant taxonomist working in the Mata Ciliar Group at NUPELIA, assisted in the identification of the plant samples and so much more detailed species lists were produced. Where appropriate, identification followed Pott and Pott (1994) and Lorenzi (2000). Names and authorities were confirmed using the W3 TROPICOS database accessed through the Missouri Botanical Garden website (www.mobot.org).

Following TWINSpan analysis, mean values of environmental, collective vegetation and dominant species trait variables were compared between TWINSpan groups using t-tests, one-way ANOVA or Kruskal-Wallis tests as appropriate.

Correlation and regression analysis of the B and C sub-site data was carried out as described in Chapter Two, Section 2.3.2. Testing of the TWINSpan results was also done in the same way. Testing of the regression relationships was limited to calculation of correlation coefficients between results predicted from 2000-2001 data and results measured in 2002. The equation explaining the greatest amount of variation, or the simpler equation if two explained similar amounts of variation, was tested with the 2002 data. Prediction by the best single variable and by the best environmental variable, if any, was also tested.

3.4 Results

3.4.1 Summary statistics and species lists

Species lists

The help of a Brazilian taxonomist (Kazue Kawakita Kita MSc.) in 2002 allowed the plant samples collected in the field to be identified with greater accuracy than in the previous two years resulting in a much more detailed species list. A few samples that were without flowers, or which had deteriorated since collection, could not be identified but most samples were identified at least to family level. The long lists of taxa presented in Table 3.4 (B) and Table 3.7 (C) were compiled from just thirteen B sub-sites and thirteen C sub-sites showing the high diversity of species across the floodplain.

The species lists compiled in 2000 and 2001 (Tables 3.1 – 3.6) are less detailed but still illustrate the range of plants observed across B and C sub-sites.

Table 3.1 2000 Bank sub-sites (B) species list

Family	Identification	Authority
Amaranthaceae	<i>Alternanthera philoxeroides</i>	(Mart.) Griseb.
Apiaceae	<i>Centella asiatica</i>	(L.) Urb.
Cecropiaceae	<i>Cecropia pachystachya</i>	Trec.
Commelinaceae	<i>Commelina</i> sp	L.
Convolvulaceae	<i>Ipomoea</i> sp	L.
Cucurbitaceae	<i>Cayaponia podantha</i>	Cogn.
Cyperaceae	<i>Cyperus brevifolius?</i>	Hassk.
Cyperaceae	<i>Cyperus giganteus</i>	Vahl.
Cyperaceae	<i>Eleocharis</i> sp	R. Br.
Cyperaceae	<i>Rhynchospora cf barbata</i>	(Vahl) Kunth
Cyperaceae	<i>Rhynchospora corymbosa</i>	(L.) Britton
Cyperaceae	<i>Rhynchospora</i> sp	Vahl.
Cyperaceae	<i>Scleria pterota</i>	Presl.
Cyperaceae		Juss.
Fabaceae	<i>Crotalaria</i> sp	L.
Fabaceae	<i>Inga</i> sp	Mill.
Fabaceae	<i>Mimosa pigra</i>	L.
Fabaceae		
Lythraceae	<i>Cuphea</i> sp	P. Browne
Malvaceae	<i>Hibiscus</i> sp	L.
Melastomataceae		Juss.
Onagraceae	<i>Ludwigia</i> sp	L.
Poaceae	<i>Andropogon bicornis</i>	L.
Poaceae	<i>Panicum pernambucense</i>	(Spreng.) Mez ex Pilg.
Poaceae	<i>Paspalum conspersum</i>	Schrad.
Poaceae	<i>Panicum prionitis</i>	Nees.
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum acuminatum</i>	Kunth
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Polygonaceae	<i>Polygonum punctatum</i>	Elliot
Polygonaceae	<i>Polygonum</i> sp	L.
Rubiaceae	<i>Galeanthe brasiliensis</i>	(Spreng.) E.L. Cabral & Bacigalupo
Rubiaceae	<i>Staelia thymoides?</i>	C. et S.
Verbenaceae	<i>Lippia alba</i>	(Mill). N.E.Brown
Vitaceae	<i>Cissus palmata</i>	Poir.
	Unidentified creepers	
	Unidentified woody plants	
	Unidentified ferns	
	Unidentified herbaceous plants	
	Unidentified saplings	
	Unidentified seedlings	

Table 3.2 2001 Temporary bank sub-sites (B1) species list

Family	Identification	Authority
Apiaceae	<i>Hydrocotyle ranunculoides</i>	L.f.
Asteraceae	<i>Conyza</i> sp	Less.
Asteraceae	<i>Gnaphalium</i> sp	L.
Asteraceae	<i>Melanthera latifolia?</i>	(Gard.) Cabrera
Asteraceae		Martinov
Commelinaceae	<i>Commelina</i> sp	L.
Convolvulaceae	<i>Cuscuta racemosa</i>	Mart.
Cucurbitaceae	<i>Cayaponia podantha</i>	Cogn.
Cyperaceae	<i>Eleocharis</i> sp	R. Br.
Cyperaceae	<i>Rhynchospora aurea?</i>	Vahl.
Cyperaceae		Juss.
Fabaceae	<i>Mimosa pigra</i>	L.
Molluginaceae	<i>Mollugo verticillata?</i>	L.
Onagraceae	<i>Ludwigia</i> sp	L.
Poaceae	<i>Paspalum repens</i>	P.J. Berguis
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Polygonaceae	<i>Polygonum</i> sp	L.
Polygonaceae	<i>Polygonum stelligerum</i>	Cham.
Pontederiaceae	<i>Eichhornia azurea</i>	(Sw.) Kunth
Pontederiaceae	<i>Eichhornia crassipes</i>	(Mart.) Solms
Salviniaceae	<i>Salvinia</i> sp	Ség.
Scrophulariaceae	<i>Scoparia montevidensis?</i>	(Spr.) Fries.
Solanaceae		Adans.
Alismataceae	<i>Sagittaria montevidensis</i>	Cham. & Schldt.
	Unidentified creepers	
	Unidentified herbaceous plants	
	Unidentified seedlings	

Table 3.3 2001 Permanent bank sub-sites (B2) species list

Family	Identification	Authority
Annonaceae	<i>Rollinia emarginata</i>	Schltld.
Asclepiadaceae	<i>Funastrum clausum</i>	(Jacq.) Schltr.
Asteraceae	<i>Conyza</i> sp	Less.
Commelinaceae	<i>Commelina</i> sp	L.
Cucurbitaceae	<i>Cayaponia podantha</i>	Cogn.
Cucurbitaceae	<i>Cayaponia</i> sp	Silva Manso
Cyperaceae	<i>Cyperus reflexus</i>	Vahl.
Cyperaceae	<i>Eleocharis</i> sp	R. Br.
Cyperaceae	<i>Rhynchospora aurea?</i>	Vahl.
Cyperaceae	<i>Scleria pterota</i>	Presl.
Cyperaceae		Juss.
Euphorbiaceae	<i>Croton urucurana</i>	Baill.
Euphorbiaceae		Juss.
Fabaceae	<i>Inga</i> sp	Mill.
Fabaceae	<i>Mimosa pigra</i>	L.
Lythraceae	<i>Cuphea</i> sp	P. Browne
Malvaceae	<i>Sida</i> sp	L.
Melastomataceae		Juss.
Onagraceae	<i>Ludwigia</i> sp	L.
Oxalidaceae	<i>Oxalis</i> sp	L.
Poaceae	<i>Andropogon bicornis</i>	L.
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Polygonaceae	<i>Polygonum stelligerum</i>	Cham.
Polygonaceae	<i>Polygonum</i> sp	L.
Pontederiaceae	<i>Eichhornia azurea</i>	(Sw.) Kunth
Pontederiaceae	<i>Pontederia cordata</i>	L.
Pteridaceae	<i>Cheilanthes</i> sp	Sw.
Rubiaceae	<i>Galeanthe brasiliensis</i>	(Spreng.) E.L. Cabral & Bacigalupo
Rubiaceae	<i>Staelia</i> sp?	Cham. & Schltld.
Scrophulariaceae		Juss.
Tiliaceae	<i>Corchorus argutus</i>	H.B.K.
Verbenaceae	<i>Lippia alba</i>	(Mill). N.E. Brown
	Unidentified creepers	
	Unidentified woody plants	
	Unidentified ferns	
	Unidentified herbaceous plants	
	Unidentified seedlings	

Table 3.4 2002 Bank sub-sites (B) species list

Family	Identification	Authority
Acanthaceae	<i>Hygrophila guianensis</i>	Nees.
Adiantaceae	cf <i>Pityrogramma calomelanos</i>	(L.) Link
Amaranthaceae	<i>Alternanthera philoxeroides</i>	(Mart.) Griseb.
Asclepiadaceae		Borkh.
Asteraceae	cf <i>Ageratum conyzoides</i>	L.
Asteraceae	cf <i>Ageratum</i> sp.	L.
Asteraceae	<i>Conyza</i> sp	Less.
Asteraceae		Martinov
Boraginaceae	<i>Heliotropium procumbens</i>	Mill.
Cecropiaceae	cf <i>Cecropia pachystachya</i>	Trec.
Commelinaceae	<i>Commelina</i> sp	L.
Convolvulaceae	cf <i>Ipomoea</i> sp	L.
Convolvulaceae	<i>Ipomoea</i> cf <i>cairica</i>	(L.) Sweet
Convolvulaceae	<i>Ipomoea</i> cf <i>rubens</i>	Choisy
Convolvulaceae	<i>Iseia luxurians</i>	(Moric.) O'Donell
Convolvulaceae		Juss.
Cucurbitaceae	<i>Cayaponia podantha</i>	Cogn.
Cucurbitaceae		Juss.
Cyperaceae	<i>Cyperus brevifolius</i>	(Rottb.) Hassk.
Cyperaceae	<i>Cyperus flavus</i>	(Vahl.) Ness.
Cyperaceae	<i>Cyperus surinamensis</i>	Rottb.
Cyperaceae	<i>Eleocharis filiculmis</i>	Kunth
Cyperaceae	<i>Eleocharis</i> sp	R. Br.
Cyperaceae	<i>Scleria pterota</i>	Presl.
Cyperaceae		Juss.
Elaeocarpaceae		Juss. ex DC.
Euphorbiaceae	cf <i>Croton</i> sp	L.
Euphorbiaceae	cf <i>Croton urucurana</i>	Baill.
Euphorbiaceae	<i>Dalechampia</i> sp	L.
Fabaceae	<i>Inga</i> sp.	Mill.
Fabaceae	<i>Mimosa pigra</i>	L.
Lythraceae	<i>Cuphea carthagenensis</i>	(Jacq.) Macbr.
Malvaceae		Adans.
Melastomataceae	<i>Clidemia</i> sp	D. Don.
Menispermaceae	<i>Cissampelus pareira</i>	L.
Menispermaceae	<i>Cissampelus</i> sp	Endl.
Onagraceae	<i>Ludwigia</i> sp	L.
Piperaceae	<i>Piper tuberculatum</i>	Jacq.
Poaceae	<i>Andropogon bicornis</i>	L.
Poaceae	cf <i>Hymenachne amplexicaulis</i>	(Rudge.) Nees.
Poaceae	cf <i>Hymenachne</i> sp	P. Beauv.
Poaceae	cf <i>Panicum sabulorum</i>	Lam.
Poaceae	<i>Digitaria</i> sp	Haller.
Poaceae	<i>Panicum decipiens</i>	Nees.
Poaceae	<i>Panicum laxum</i>	SW.
Poaceae	<i>Panicum sabulorum</i>	Lam.
Poaceae	<i>Panicum stoloniferum</i>	Poiret
Poaceae	<i>Paspalum</i> cf <i>conjugatum</i>	Berguis
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum acuminatum</i>	Kunth
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Polygonaceae	<i>Polygonum punctatum</i>	Elliott
Polygonaceae	<i>Polygonum stelligerum</i>	Cham.
Pteridaceae	<i>Adiantum latifolium</i>	Lam.
Rubiaceae	<i>Galeanthe brasiliensis</i>	(Spreng.) E.L. Cabral & Bacigalupo

Table 3.4 continued 2002 Bank sub-sites (B) species list

Family	Identification	Authority
Rubiaceae	<i>Palicourea cf crocea</i>	(SW.) Roem. et Schultes
Verbenaceae	<i>Lippia alba</i>	(Mill.) N.E. Brown
Verbenaceae		Adans.
Vitaceae	<i>Cissus palmata</i>	Poir.
	Unidentified creepers	
	Unidentified ferns	
	Unidentified woody plants	
	Unidentified herbaceous plants	
	Unidentified seedlings	

Table 3.5 2000 Floodplain sub-sites (C) species list

Family	Identification	Authority
Asteraceae	<i>Artemisia</i> sp?	L.
Asteraceae	<i>Aspilia latissima</i>	Malme
Asteraceae	<i>Conyza</i> sp	Less.
Asteraceae	<i>Eupatorium</i> cf <i>laevigatum</i>	Lam.
Asteraceae	<i>Eupatorium pauciflorum</i>	Kunth
Asteraceae	<i>Gnaphalium</i> sp	L.
Asteraceae	<i>Orthopappus angustifolius?</i>	(Sw.) Gl.
Asteraceae		Martinov
Cecropiaceae	<i>Cecropia pachystachya</i>	Trec.
Commelinaceae	<i>Commelina</i> sp	L.
Convolvulaceae	<i>Ipomoea</i> sp	L.
Cucurbitaceae		Juss.
Cyperaceae	<i>Cyperus ferax?</i>	Rich.
Cyperaceae	<i>Cyperus giganteus</i>	Vahl.
Cyperaceae	<i>Cyperus sesquiflorus?</i>	(Torrey) Mattf. & Kiik.
Cyperaceae	<i>Scleria pterota</i>	Presl.
Cyperaceae		Juss.
Fabaceae	<i>Crotalaria</i> sp	L.
Fabaceae	<i>Inga</i> sp	Mill.
Fabaceae	<i>Mimosa pigra</i>	L.
Fabaceae		
Lythraceae	<i>Cuphea racemosa?</i>	(L.f.) Spreng.
Malvaceae	<i>Sida</i> sp	L.
Marantaceae	<i>Thalia geniculata</i>	L.
Onagraceae	<i>Ludwigia</i> sp	L.
Poaceae	<i>Cynodon</i> sp	Rich.
Poaceae	<i>Panicum grande</i>	Hitchc. & Chase.
Poaceae	<i>Panicum pernambucense</i>	(Spreng.) Mez. ex Pilg.
Poaceae	<i>Sorghum halepense</i>	(L.) Pers.
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum acuminatum</i>	Kunth
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Rubiaceae	<i>Diodia</i> sp	L.
Rubiaceae	<i>Galeanthe brasiliensis</i>	(Spreng.) E.L. Cabral & Bacigalupo
Solanaceae		Adans.
Verbenaceae	<i>Lippia alba</i>	(Mill.) N.E.Brown
	Unidentified creepers	
	Unidentified woody plants	
	Unidentified herbaceous plants	
	Unidentified saplings	
	Unidentified seedlings	

Table 3.6 2001 Floodplain sub-sites (C) species list

Family	Identification	Author
Asclepiadaceae	<i>Funastrum clausum</i>	(Jacq.) Schltr.
Asteraceae	<i>Conyza</i> sp	Less.
Asteraceae	<i>Orthopappus angustifolius?</i>	(Sw.) Gl.
Commelinaceae	<i>Commelina</i> sp	L.
Convolvulaceae	<i>Ipomoea cairica</i>	(L.) Sweet
Cucurbitaceae	<i>Cayaponia</i> sp	Silva. Manso
Cyperaceae	<i>Cyperus giganteus</i>	Vahl.
Cyperaceae	<i>Eleocharis</i> sp	R. Br.
Cyperaceae	<i>Scleria pterota</i>	Presl.
Cyperaceae		Juss.
Euphorbiaceae	<i>Croton urucurana</i>	Baill.
Euphorbiaceae	<i>Sapium longifolium?</i>	(Müll. Arg.) Huber
Fabaceae	<i>Inga</i> sp	Mill.
Fabaceae	<i>Mimosa</i> sp	L.
Marantaceae	<i>Thalia geniculata</i>	L.
Onagraceae	<i>Ludwigia</i> sp	L.
Poaceae	<i>Andropogon bicornis</i>	L.
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Polygonaceae	<i>Polygonum stelligerum</i>	Cham.
Polygonaceae	<i>Polygonum</i> sp	L.
Rubiaceae	<i>Galeanthe brasiliensis</i>	(Spreng.) E.L. Cabral & Bacigalupo
Rubiaceae	<i>Palicourea crocea</i>	(Sw.) Roem. & Schult.
Rubiaceae	<i>Staelia</i> sp?	Cham. & Schltldl.
Smilacaceae	<i>Smilax</i> sp	Gris.
Verbenaceae	<i>Lippia alba</i>	(Mill.) N.E. Brown
	Unidentified creepers	
	Unidentified woody plants	
	Unidentified ferns	
	Unidentified herbaceous plants	
	Unidentified saplings	
	Unidentified seedlings	

Table 3.7 2002 Floodplain sub-sites (C) species list

Family	Identification	Authority
Amaranthaceae	<i>Pfaffia glomerata</i>	(Sprengel.) Pedersen
Annonaceae	<i>Rollinia emarginata</i>	Schlecht
Apocynaceae	<i>Prestonia cf dusenii</i>	(Malme.) Woodson
Asclepiadaceae		Borkh.
Asteraceae	<i>Eupatorium</i> sp	L.
Asteraceae	<i>Porophyllum ruderale</i>	(Jacq.) Cass.
Buddlejaceae		K. Wilh.
Clusiaceae	<i>Garcynia gardneriana</i>	(Pl. et Tr.) Zappi
Commelinaceae	<i>Commelina</i> sp	L.
Convolvulaceae	<i>Ipomoea cf rubens</i>	Choisy
Convolvulaceae	<i>Iseia luxurians</i>	(Moric.) O'Donell
Convolvulaceae		Juss.
Cucurbitaceae	<i>cf Cayaponia podantha</i>	Cogn.
Cucurbitaceae	<i>cf Momordica</i> sp.	L.
Cyperaceae	<i>Scleria pterota</i>	Presl.
Cyperaceae		Juss.
Elaeocarpaceae		Juss. ex DC.
Euphorbiaceae	<i>Dalechampia</i> sp	L.
Fabaceae	<i>Mimosa pigra</i>	L.
Fabaceae		
Malvaceae	<i>Hibiscus cisplatimus</i>	St. Hil.
Onagraceae	<i>Ludwigia</i> sp	L.
Onagraceae		
Poaceae	<i>Andropogon bicornis</i>	L.
Poaceae	<i>cf Hymenachne amplexicaulis</i>	(Rudge.) Nees.
Poaceae	<i>Oplismenus hirtellus</i>	(L.) Beauv.
Poaceae	<i>cf Oplismenus</i> sp	P. Beauv.
Poaceae	<i>Panicum pernambucense</i>	(Spreng.) Mez.
Poaceae	<i>Panicum stoloniferum</i>	Poir.
Poaceae	<i>Paspalum conspersum</i>	Schrader ex. Schultes
Poaceae		(R. Br.) Barnhart
Polygonaceae	<i>Polygonum acuminatum</i>	Kunth
Polygonaceae	<i>Polygonum ferrugineum</i>	Wedd.
Polygonaceae	<i>Polygonum stelligerum</i>	Cham.
Rubiaceae	<i>Galeanthe brasiliensis</i>	(Spreng.) E.L. Cabral & Bacigalupo
Rubiaceae	<i>Psychotria cf leiocarpa</i>	Cham. et Schl.
Sapindaceae	<i>Allophylus edulis</i>	(A. St. Hil. & al) Radlk.
Sapindaceae	<i>cf Paullinia spicata</i>	Benth.
Smilacaceae	<i>Smilax</i> sp.	L.
Sterculiaceae	<i>Melochia arenosa</i>	Benth.
Verbenaceae	<i>Lippia alba</i>	(Mill.) N.E. Brown
	Unidentified woody plants	
	Unidentified herbaceous plants	
	Unidentified seedlings	

Summary data

The following twelve tables summarise the environmental, collective vegetation and dominant species trait data collected at B sub-sites in 2000, 2001 and 2002.

2000 B**Table 3.8 Minimum, maximum and median or mode values of each environmental variable measured at 19 bank sub-sites in 2000.**

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	1	15	3	
Elevation above water (m)	0.1	2.5	0.5	
Soil pH	3.80	5.70	4.80	
Soil total Kjeldahl N (mgkg ⁻¹)	320	9450	2580	
Soil ADAS ext. P (mgkg ⁻¹)	2.73	56.69	12.84	
Soil total Fe (mgkg ⁻¹)	22900	70200	42400	
Soil total Ca (mgkg ⁻¹)	215	2040	932	
Openness (1-5)	1	3		3
Grazing intensity (1-5)	1	2		1
Shade (1-5)	1	4		1

Table 3.9 Minimum, maximum and median values of each collective vegetation variable measured at 19 bank sub-sites in 2000.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	4	22	8
Dry weight biomass (gm ⁻²)	71.00	2624.12	652.38
Canopy height (m)	0.17	1.65	1.07
Canopy cover (%)	22	100	60.56
Stem density (m ⁻²)	100	2611	455.56

Table 3.10 Minimum, maximum and median values of each dominant species trait variable measured at 19 bank sub-sites in 2000.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.50	18.07	2.53
Total root dry weight per plant (g)	0.01	4.38	0.51
Remainder dry weight per plant (g)	0.12	36.70	7.35
Total plant dry weight (g)	0.74	46.20	10.37
Maximum stem length (m)	0.30	1.95	1.50
Total leaf area per plant (cm ²)	127.76	2711.33	301.23
Specific leaf area (cm ² g ⁻¹)	69.84	493.81	141.96
Leaf weight / root weight ratio	0.42	367.00	4.45

2001 B1**Table 3.11 Minimum, maximum and median or mode values of each environmental variable measured at 13 B1 bank sub-sites in 2001.**

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	1	5	4	
Elevation above water (m)	0.1	1.0	0.2	
Soil pH	4.00	6.70	5.31	
Soil total Kjeldahl N (mgkg ⁻¹)	241	14990	2074	
Soil ADAS ext. P (mgkg ⁻¹)	3.14	53.33	12.18	
Soil total Fe (mgkg ⁻¹)	9263	104497	42667	
Soil total Ca (mgkg ⁻¹)	161	6151	1770	
Openness (1-5)	1	3		2
Grazing intensity (1-5)	1	5		1
Shade (1-5)	1	2		1

Table 3.12 Minimum, maximum and median values of each collective vegetation variable measured at 13 B1 bank sub-sites in 2001.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	4	25	11
Dry weight biomass (gm ⁻²)	21.8	873.8	151.0
Canopy height (m)	0.08	1.03	0.18
Canopy cover (%)	3.56	71.11	44.44
Stem density (m ⁻²)	55.56	800	344.44

Table 3.13 Minimum, maximum and median values of each dominant species trait variable measured at 13 B1 bank sub-sites in 2001.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.09	33.91	0.82
Remainder dry weight per plant (g)	0.07	24.13	0.56
Total plant dry weight (g)	0.19	58.04	1.36
Maximum stem length (m)	0.08	0.95	0.25
Total leaf area per plant (cm ²)	23.70	2722.38	244.74
Specific leaf area (cm ² g ⁻¹)	80.28	3106.77	253.28

2001 B2**Table 3.14 Minimum, maximum and median or mode values of each environmental variable measured at 19 B2 bank sub-sites in 2001.**

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	0.5	30	5	
Elevation above water (m)	0.2	4.0	0.7	
Soil pH	4.00	6.90	5.10	
Soil total Kjeldahl N (mgkg ⁻¹)	350	27447	2623	
Soil ADAS ext. P (mgkg ⁻¹)	5.73	50.00	22.76	
Soil total Fe (mgkg ⁻¹)	8824	89555	47160	
Soil total Ca (mgkg ⁻¹)	143	10335	1776	
Openness (1-5)	1	3		1
Grazing intensity (1-5)	1	5		1
Shade (1-5)	1	3		1

Table 3.15 Minimum, maximum and median values of each collective vegetation variable measured at 19 B2 bank sub-sites in 2001.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	2	19	9
Dry weight biomass (gm ⁻²)	83.76	1401.64	371.32
Canopy height (m)	0.10	1.50	0.77
Canopy cover (%)	13.89	98.89	76.11
Stem density (m ⁻²)	166.67	2633.33	388.89

Table 3.16 Minimum, maximum and median values of each dominant species trait variable measured at 19 B2 bank sub-sites in 2001.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.24	6.53	2.98
Remainder dry weight per plant (g)	0.37	9.50	3.23
Total plant dry weight (g)	0.61	14.09	5.76
Maximum stem length (m)	0.13	1.42	0.82
Total leaf area per plant (cm ²)	33.27	802.42	413.37
Specific leaf area (cm ² g ⁻¹)	41.58	200.60	141.04

2002 B**Table 3.17 Minimum, maximum and median or mode values of each environmental variable measured at 13 bank sub-sites in 2002.**

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	0.5	7	2	
Elevation above water (m)	0.1	1.5	0.4	
Soil pH	3.87	6.15	4.98	
Soil total Kjeldahl N (mgkg ⁻¹)	540	10300	3370	
Soil ADAS ext. P (mgkg ⁻¹)	4.25	58.65	11.11	
Soil total Fe (mgkg ⁻¹)	17400	106000	30200	
Soil total Ca (mgkg ⁻¹)	372	2090	1080	
Openness (1-5)	1	4		2
Grazing intensity (1-5)	1	2		1
Shade (1-5)	1	4		1

Table 3.18 Minimum, maximum and median values of each collective vegetation variable measured at 13 B bank sub-sites in 2002.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	2	19	11
Dry weight biomass (gm ⁻²)	116.72	2520.52	628.38
Canopy height (m)	0.21	1.22	0.95
Canopy cover (%)	47.22	100	92.22
Stem density (m ⁻²)	211.11	6033.33	677.78

Table 3.19 Minimum, maximum and median values of each dominant species trait variable measured at 13 B bank sub-sites in 2002.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.16	2.85	1.2
Remainder dry weight per plant (g)	0.56	19.93	3.54
Total plant dry weight (g)	0.72	22.67	4.12
Maximum stem length (m)	0.30	1.80	0.90
Total leaf area per plant (cm ²)	28.07	384.54	181.45
Specific leaf area (cm ² g ⁻¹)	87.72	300.01	157.01

The following nine tables summarise the environmental, collective vegetation and dominant species trait data collected at C sub-sites in 2000, 2001 and 2002.

2000 C

Table 3.20 Minimum, maximum and median or mode values of each environmental variable measured at 19 floodplain sub-sites in 2000.

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	3	200	20	
Elevation above water (m)	0.5	4.0	2.0	
Soil pH	3.80	6.90	4.70	
Soil total Kjeldahl N (mgkg ⁻¹)	240	5320	2450	
Soil ADAS ext. P (mgkg ⁻¹)	3.76	47.57	12.35	
Soil total Fe (mgkg ⁻¹)	14000	63600	47400	
Soil total Ca (mgkg ⁻¹)	418	2550	929	
Openness (1-5)	1	5		1
Grazing intensity (1-5)	1	5		1
Shade (1-5)	1	5		1

Table 3.21 Minimum, maximum and median values of each collective vegetation variable measured at 19 floodplain sub-sites in 2000.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	4	22	9
Dry weight biomass (gm ⁻²)	24.00	1712.72	312.12
Canopy height (m)	0.03	2.03	0.41
Canopy cover (%)	8.11	100	78.33
Stem density (m ⁻²)	77.78	1955.56	444.44

Table 3.22 Minimum, maximum and median values of each dominant species trait variable measured at 19 floodplain sub-sites in 2000.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.01	21.56	1.03
Remainder dry weight per plant (g)	0.01	21.73	3.11
Total plant dry weight per plant (g)	0.03	37.54	4.39
Maximum stem length (m)	0.02	2.29	0.67
Total leaf area per plant (cm ²)	2.02	2667.45	212.48
Specific leaf area (cm ² g ⁻¹)	41.78	531.14	237.95

2001 C**Table 3.23 Minimum, maximum and median or mode values of each environmental variable measured at 20 floodplain sub-sites in 2001.**

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	4	50	10	
Elevation above water (m)	0.5	4.0	1.25	
Soil pH	4.00	6.30	4.60	
Soil total Kjeldahl N (mgkg ⁻¹)	533	34884	2867	
Soil ADAS ext. P (mgkg ⁻¹)	8.19	63.66	24.08	
Soil total Fe (mgkg ⁻¹)	13196	93605	40239	
Soil total Ca (mgkg ⁻¹)	325	9070	1204	
Openness (1-5)	1	5		1
Grazing intensity (1-5)	1	5		1
Shade (1-5)	1	4		1

Table 3.24 Minimum, maximum and median values of each collective vegetation variable measured at 20 floodplain sub-sites in 2001.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	1	13	6.5
Dry weight biomass (gm ⁻²)	47.94	1795.04	509.47
Canopy height (m)	0.21	1.72	0.74
Canopy cover (%)	10.56	100	59.45
Stem density (m ⁻²)	77.78	688.89	366.67

Table 3.25 Minimum, maximum and median values of each dominant species trait variable measured at 20 floodplain sub-sites in 2001.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.37	9.29	1.88
Remainder dry weight per plant (g)	0.39	17.45	3.74
Total plant dry weight (g)	1.09	26.74	5.28
Maximum stem length (m)	0.33	1.49	0.94
Total leaf area per plant (cm ²)	62.70	1449.24	313.32
Specific leaf area (cm ² g ⁻¹)	95.95	1226.93	157.08

2002 C**Table 3.26 Minimum, maximum and median or mode values of each environmental variable measured at 13 floodplain sub-sites in 2002.**

Variable	Minimum	Maximum	Median	Mode
Distance from water (m)	6	20	10	
Elevation (m)	0.3	4.0	2.5	
Soil pH	3.98	5.59	4.77	
Soil total Kjeldahl N (mgkg ⁻¹)	1090	14700	1910	
Soil ADAS ext. P (mgkg ⁻¹)	4.29	35.05	9.18	
Soil total Fe (mgkg ⁻¹)	16200	71000	30000	
Soil total Ca (mgkg ⁻¹)	418	3870	768	
Openness (1-5)	1	5		1
Grazing intensity (1-5)	1	1		1
Shade (1-5)	1	4		1

Table 3.27 Minimum, maximum and median values of each collective vegetation variable measured at 13 floodplain sub-sites in 2002.

Variable	Minimum	Maximum	Median
Number of species (per sub-site)	3	14	8
Dry weight biomass (gm ⁻²)	44.20	1711.64	1111
Canopy height (m)	0.19	1.83	1.06
Canopy cover (%)	23.33	100	85.56
Stem density (m ⁻²)	66.67	1355.56	244.44

Table 3.28 Minimum, maximum and median values of each dominant species trait variable measured at 13 floodplain sub-sites in 2002.

Variable	Minimum	Maximum	Median
Total leaf dry weight per plant (g)	0.16	11.83	2.01
Remainder dry weight per plant (g)	0.21	16.3	5.56
Total plant dry weight (g)	0.37	19.82	8.93
Maximum stem length (m)	0.35	2.07	1.17
Total leaf area per plant (cm ²)	45.46	1138.55	314.37
Specific leaf area (cm ² g ⁻¹)	96.24	419.90	181.23

3.4.2 Identification of bank vegetation communities

TWINSPAN analysis of 2000 bank data

TWINSPAN analysis of vegetation data collected from banks and shores of floodplain waterbodies in 2000 produced two main groups of sites. At the first division, two unusual sites (LP and POU) were split off from the main group with an eigenvalue of 0.613 due to the presence of *Polygonum acuminatum* at these two sites. At the second division, a single site (LOS) was split off with an eigenvalue of 0.507 due to the presence of a rarely recorded taxon, *Cuphea* sp. LOS and POU were also unusual in that they were the only two sub-sites with evidence of grazing. The remaining fifteen sites were divided at the third division into a group of eight (group II), indicated by *Commelina* sp. and *Ludwigia* sp., and a group of seven (group I) in which these species tended to be absent. The eigenvalue for this division was 0.410.

Comparisons of TWINSPAN groups

Site locations and species compositions

There was no clear pattern of river association or bank type between the two main TWINSPAN groups. Each group included sites on the Baía and on the Paraná Rivers with a mixture of gently sloping shores and steep banks.

The association of group II sites with *Commelina* sp., *Ludwigia* sp. and *Polygonum* sp. suggested that this was a wetter community than that found in group I sites in which more terrestrial plants, such as the creeper *Cissus* sp. and tree saplings, tended to occur. The lower elevation of group II sites suggests a greater availability of water for wetland species at these sites than at group I sites (Table 3.30). Table 3.29 lists the contrasting characteristics between groups I and II.

Table 3.29 Summary of contrasting 2000 B TWINSPAN group characteristics.

TWINSPAN group	I	II
Number of sites	7	8
Indicator species	None	Presence of <i>Commelina</i> sp. and <i>Ludwigia</i> sp.
Predominant river association	Baía and Paraná	Baía and Paraná
Environmental characteristics	Higher elevation, lower soil Ca	Lower elevation, higher soil Ca
Vegetation characteristics	Shorter canopy height	Taller canopy height
Traits of dominant species	Similar between groups	

Environmental comparisons

Comparison of environmental variables measured at the bank sub-sites in each group showed that group I sites tended to be at a higher elevation above the associated water body than group II sites (Table 3.30). The soil at group I sites had a significantly lower total calcium content than the soil at group II sites (Table 3.30). None of the other measured variables differed significantly between the groups. There was no evidence of grazing at the sub-sites in either of the TWINSPAN groups and the most frequent open-ness score was three (moderate open-ness) in both groups. The most frequently recorded shade score was one (*i.e.*, no shade) in both groups, although group I included more shaded sub-sites than group II.

Table 3.30 Mean, standard error (S.e.) and significance of differences (t-tests) between 2000 B TWINSPAN groups of normally distributed environmental variables (data back-transformed as necessary to give original values).

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Distance from water (m)	2.64	0.54	3.00	0.65	0.789
Elevation above water (m)	1.02	0.33	0.36	0.11	0.054
Soil pH	5.00	0.16	4.85	0.16	0.523
Soil ADAS ext. P (mgkg ⁻¹)	14.01	5.52	15.55	4.79	0.703
Soil total Kjeldahl N (mgkg ⁻¹)	2369	855	2980	1013	0.489
Soil total Fe (mgkg ⁻¹)	42029	3483	43188	5315	0.863
Soil total Ca (mgkg ⁻¹)	743	152	1302	198	0.048

Collective vegetation comparisons

Canopy height, number of species, dry weight biomass and canopy cover were all greater in group II than in group I but canopy height was the only variable close to being significantly different between the two groups (Table 3.31).

Table 3.31 Means, standard errors and significance of differences (t-tests) between 2000 B TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	9.14	1.8	10.88	2.2	0.561
Dry weight biomass (gm ⁻²)	689.23	208.33	937.57	276.93	0.430
Canopy height (m)	0.81	0.17	1.24	0.11	0.053
Canopy cover (%)	52.5	13	63.2	7.8	0.469
Stem density (m ⁻²)	782.54	256.88	593.06	107.75	0.951
Total leaf dry weight per plant (g)	3.64	1.26	4.46	1.96	0.506
*Total leaf area per plant (cm ²)	313.1		304.4		0.908
Total root dry weight per plant (g)	1.00	0.42	0.97	0.58	0.808
Remainder dry weight per plant (g)	9.97	4.96	10.72	1.74	0.393
Total plant dry weight (g)	14.5	6.3	16.03	7.52	0.815
Leaf weight/ root weight	16.27	8.87	57.57	51.59	0.643
*Maximum stem length (m)	1.50		1.52		0.416

Comparisons of traits of dominant species

Total leaf weight, remainder weight and total plant weight were all greater in group II than in group I but these differences were not statistically significant (Table 3.31).

TWINSpan analysis of 2001 B1 bank data

The thirteen B1 sub-sites encountered in 2001 considered to be temporary banks exposed due to the particularly low river level provided a very small data set for TWINSpan analysis. However, after division one split off one site from the main group because it was unusual in supporting a mainly aquatic species, *Paspalum repens* (eigenvalue = 0.554), division two produced two groups of sites which it seemed reasonable to compare due to their contrasting species assemblages and moderately high eigenvalue of 0.420. This division produced a group of seven (group I), indicated by moderately abundant *Polygonum ferrugineum* and very abundant *Cyperus* sp., and a group of four (group II),

indicated by the presence of *Eleocharis* sp. and unidentified herbaceous plants and by moderately abundant *Ludwigia* sp..

Comparisons of TWINSpan groups

Site locations and species compositions

Table 3.32 summarises the contrasting characteristics of TWINSpan groups I and II. The locations of the sub-sites were mixed in both groups but all three Ivinheima sub-sites occurred together in group I. The reason for the choice of indicator species by TWINSpan was clear from the output table which showed obvious patterns in the occurrence or abundance of these species. However, there were also several rare species that were restricted to one group or the other. The low overall frequency of these species could mean that they are absent from some sites by chance rather than because growth conditions are unsuitable. Their influence on the analysis could therefore be misleading.

Table 3.32 Summary of contrasting 2001 B1 TWINSpan group characteristics.

TWINSpan group	I	II
Number of sites	7	4
Indicator species	Moderately abundant <i>Polygonum ferrugineum</i> , very abundant Cyperaceae.	<i>Commelina</i> sp. and <i>Ludwigia</i> sp. present.
Predominant river association	Ivinheima, Baía, Paraná	Baía, Paraná
Environmental characteristics	Similar between groups	
Vegetation characteristics	Similar between groups	
Traits of dominant species	Similar between groups	

Environmental comparisons

None of the measured environmental variables differed significantly between the two TWINSpan groups. Sub-sites were open (mainly scores one and two) and unshaded (mainly score one) in both groups. Grazing was slightly more important in group II, with two sub-sites scoring three and five (moderate and intense grazing), while group I sub-sites all scored one or two. Grazing may have contributed to the difference in community between the two TWINSpan groups. However, the general similarity of the measured environmental variables between the two groups could suggest that important environmental variables or other types of variables (for example, variables connected with disturbances, such as fire) were not measured. Alternatively, there may not have been two

distinct vegetation communities at B1 sub-sites, with the sub-sites in this small data set perhaps representing variations on a single, larger community (Table 3.33).

Table 3.33 Mean, standard error (S.e.) and significance of differences (t-tests) between 2001 B1 TWINSpan groups of normally distributed environmental variables (data back-transformed as necessary to give original values).

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Distance (m)	3.43	0.65	2.50	0.65	0.375
Elevation (m)	0.44	0.31	0.18	0.05	0.106
Soil pH	5.15	0.34	5.75	0.48	0.326
Soil ADAS ext. P (mgkg ⁻¹)	20.68	4.76	19.39	11.41	0.905
Soil total Kjeldahl N (mgkg ⁻¹)	4432	1918	2251	1051	0.567
Soil total Fe (mgkg ⁻¹)	42452	8898	45086	12023	0.863
Soil total Ca (mgkg ⁻¹)	2026	394	1036	347	0.154

Collective vegetation comparisons and comparisons of dominant species traits

None of the collective vegetation variables or dominant species trait variables differed significantly between the two TWINSpan groups, again suggesting that these did not represent distinct vegetation communities (Table 3.34).

Table 3.34 Means, standard errors and significance of differences (t-tests) between 2001 B1 TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values).

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	10	1.9	13	4.4	0.477
Dry weight biomass (gm ⁻²)	275.93	108.55	162.02	37.22	0.800
Canopy height (m)	0.38	0.13	0.16	0.05	0.185
Canopy cover (%)	50.27	6.84	45.00	7.68	0.637
Stem density (m ⁻²)	404.76	70.39	483.33	132.13	0.575
Total leaf dry weight per plant (g)	6.62	5.48	0.86	0.30	0.323
Total leaf area per plant (cm ²)	725.46	416.40	184.93	59.38	0.404
Remainder dry weight per plant (g)	4.30	3.97	0.70	0.35	0.699
Total plant dry weight (g)	12.38	11.42	1.56	0.60	0.447
Maximum stem length (m)	0.48	0.16	0.22	0.06	0.912

TWINSPAN analysis of 2001 B2 bank data

The nineteen permanent bank sub-sites (B2) surveyed in 2001 were grouped using TWINSPAN analysis. The first division formed a group of eight sub-sites (group I), indicated by the presence of Poaceae and by moderately abundant creepers, and a group of eleven sites (group II), indicated by moderately abundant *Polygonum* sp.. The eigenvalue for this division was high (0.686), meaning that the two groups of sites were substantially different in species assemblage. Each of the indicator species occurred at several sites and so the divisions based upon their distribution are more likely to be reliable than any based on rarer species. At the second level of division, group I was split into two groups of four sub-sites. The eigenvalue was moderately high (0.540). Group Ia was indicated by the presence of *Andropogon bicornis* and unidentified woody plants while these were absent from group Ib. Group II was split into a group of five sub-sites (group IIa), indicated by the presence of *Polygonum stelligerum*, and a group of six sub-sites (group IIb) from which this species was absent.

Comparisons of TWINSPAN groups

Site locations and species compositions

The two levels of division considered in the analysis had high eigenvalues indicating that the resulting groups were substantially different in their species assemblages. During the first division, sub-sites supporting many of the more terrestrial plant groups were placed in group I (grasses, creepers, ferns) and the more amphibious plants in group II (*Polygonum* sp., *P. ferrugineum*, *P. stelligerum*, *Ludwigia* sp.) although there was some overlap. In the second division, eigenvalues dropped but there were still some good indicators of the four resulting groups. Several rare species occurred exclusively in group Ia, the least rare of these being *Andropogon bicornis*, which occurred in three out of the four sites in this group. Like group Ib, Poaceae was common and *Polygonum* sp. was rare. Group Ib differed from Ia because of the absence of *Andropogon* and the woody plant group and because it had a different set of rarely recorded species. The greatest contrast in groups I and II was the tendency of Poaceae to occur only in group I (present at only one sub-site in group II) and *Polygonum* sp. to occur only in group II (present at only two sub-sites at low abundance in group I). *Polygonum stelligerum* was associated with group IIa sites (absent from IIb) while *Ludwigia* sp. was more common in group IIb sites than group IIa.

The major division of the nineteen sub-sites into group I and group II corresponds with a contrast in the type of channel to which the sub-sites were adjacent. Five out of eight sub-

sites in group I were located at the edge of flowing channels while this was the case for only one out of eleven sub-sites in group II. Instead, group II sub-sites were mostly at the edge of open lagoons or backwaters (nine out of eleven). There was a slightly less clear pattern in the channel with which each group was associated. Five out of eight sub-sites in group I were associated with the Paraná River and only three out of eleven in group II. Group II sites were evenly distributed between the Paraná, Baía and Ivinheima Rivers.

The differences between the four TWINSpan groups are summarised in Table 3.35.

Table 3.35 Summary of contrasting 2001 B2 TWINSpan group characteristics.

TWINSpan group	Ia	Ib	IIa	IIb
Number of sites	4	4	5	6
Indicator species	<i>Andropogon bicornis</i> and woody plants present.	<i>A. bicornis</i> and woody plants absent.	<i>Polygonum stelligerum</i> present.	<i>P. stelligerum</i> absent.
Predominant river association	Paraná, Baía	Paraná	Ivinheima	Paraná, Baía
Environmental characteristics	Less acidic soil pH, low soil P, N and Ca, open, unshaded.	Intermediate soil pH, P, N and Ca, open, unshaded.	More acidic soil pH, high P, N and Ca, less open, more shaded.	Less acidic soil pH, intermediate P, N and Ca, less open, more shaded.
Vegetation characteristics	High species richness.	Intermediate species richness.	Low species richness.	Intermediate species richness.
Traits of dominant species	Similar			

Environmental comparisons

Four of the measured environmental variables differed significantly between the TWINSpan groups, suggesting that these may influence (or be related to unmeasured variables which influence) the observed distribution of species across the sub-sites (Table 3.36). Group IIa had particularly high soil phosphorus, nitrogen and calcium and particularly low pH. Soil pH was significantly lower than in groups Ia and IIb. Soil phosphorus was significantly greater than in any of the other groups. Group IIb soil phosphorus was also significantly greater than group Ia. Soil nitrogen and calcium were significantly greater in group IIa than group Ia. The grazing scores were similar between groups (most frequently one, *i.e.*, no grazing). Groups Ia and Ib included more shaded sub-

sites (scores two or three), and were correspondingly less open, than groups IIa and IIb in which all sub-sites were unshaded.

Table 3.36 Means, standard errors and significance of differences (one-way ANOVA) between 2001 B2 TWINSpan groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons).

Variable	Group Ia		Group Ib		Group IIa		Group IIb		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Distance from water (m)	5.00	1.91	7.13	2.54	4.80	2.62	10.17	4.04	0.450
Elevation above water (m)	1.89	0.75	0.80	0.24	0.80	0.21	0.72	0.27	0.200
Soil pH	5.65 ^a	0.22	5.11 ^{ab}	0.15	4.55 ^b	0.18	5.64 ^{ac}	0.32	0.019
Soil ADAS ext. P (mgkg ⁻¹)	8.19 ^a	1.02	19.31 ^{ac}	3.27	35.08 ^b	4.34	21.09 ^c	1.87	<0.001
Soil total Kjeldahl N (mgkg ⁻¹)	697 ^a	153	3485 ^{ab}	1249	13084 ^b	4428	7179 ^{ab}	3214	0.013
Soil total Fe (mgkg ⁻¹)	33070	10666	41040	6292	57057	9337	58826	12530	0.308
Soil total Ca (mgkg ⁻¹)	578 ^a	102	1184 ^{ab}	297	4498 ^b	1599	2894 ^{ab}	854	0.051

Collective vegetation comparisons

The contrasts in species assemblages between groups were not matched by variation in the collective physical characteristics of the vegetation. Only one of the variables measured for the vegetation as a whole differed significantly between TWINSpan groups, *i.e.*, species richness which was significantly greater in group Ia than in group IIa (Table 3.37).

Comparisons of traits of dominant species

Despite the different array of species in each group, the mean values of the measured trait variables did not differ significantly between the TWINSpan groups (Table 3.37).

Table 3.37 Means, standard errors and significance of differences (one-way ANOVA) between 2001 B2 TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Ia		Ib		IIa		IIb		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
No. of species (per sub-site)	15.50 ^a	7.75	8.25 ^{ab}	4.13	7.00 ^b	3.13	8.67 ^{ab}	1.36	0.023
Dry weight biomass (gm ⁻²)	339.66	169.83	701.26	350.63	448.26	200.47	397.62	77.84	0.841
Canopy height (m)	0.93	0.47	0.65	0.33	0.71	0.32	0.73	0.16	0.819
Canopy cover (%)	64.44	32.22	60.83	30.42	72.56	32.45	83.61	5.27	0.346
*Stem density (m ⁻²)	555.6		416.7		311.1		427.8		0.228
Total leaf dwt per plant (g)	2.67	1.31	1.96	0.98	2.71	1.21	3.88	0.39	0.421
Total leaf area per plant (cm ²)	346.82	161.23	280.62	140.31	376.99	168.60	602.46	89.11	0.244
Specific leaf area (cm ² g ⁻¹)	152.55	15.52	142.72	71.36	145.20	64.94	153.05	15.69	0.933
Remainder dwt per plant (g)	3.54	0.24	2.37	1.19	4.00	1.79	4.59	0.63	0.150
Total plant dry weight (g)	6.21	1.50	4.33	2.17	6.90	3.08	8.47	0.92	0.400
Maximum stem length (m)	1.00	0.18	0.68	0.24	0.80	0.10	0.65	0.13	0.460

TWINSpan analysis of 2001 B1 and B2 bank data

Combining the temporary bank (B1) and permanent bank (B2) data sets gave a much larger data set covering a wider range of bank types than the individual groups. TWINSpan analysis was applied to 31 sub-sites (BIL B1 was not included because there was little species data for this site). The first TWINSpan division had a high eigenvalue of 0.602 and split off eight sites although one of these, CUR3 B2, was misclassified. Group I consisted of the remaining seven sites and was indicated by abundant Poaceae, moderately abundant creepers and by the presence of *Inga* sp.. The large group of 23 was indicated by the presence of *Polygonum* sp. and *Ludwigia* sp.. At the second division, group I was further divided into small groups and a single site was split off from the group of 23. In

the third division, the 22 sites were split into two groups of eleven, one indicated by the presence of *Cyperus* sp. (group II) and the other indicated by the absence of this genus (group III). The eigenvalue for this division was 0.399. The three large groups which had been produced by this stage in the analysis were selected for comparison to allow large scale differences in vegetation type to be investigated. These could have been disguised if the divisions were continued and smaller groups produced.

Comparisons of TWINSpan groups

Site locations and species compositions

In 2001, bank sub-sites were classified according to whether they were appeared to be permanent banks (normally exposed during the dry season and so supporting established vegetation) or temporary banks (areas apparently normally submerged during the dry season, but exposed in 2001 due to an exceptionally low river level and therefore with a lot of bare ground or apparently recent plant colonisation). B1 sub-sites were always closer to the waterbody and at lower elevation than corresponding B2 sub-sites. TWINSpan analysis showed that there were real differences in these types of banks because site groupings corresponded with the bank classification. Group II comprised almost entirely B1 sub-sites while groups I and III were mainly B2 sub-sites. Groups I and III differed in their associations with particular rivers and channel types. Group I sub-sites were associated with the Paraná River (four of seven sub-sites) and with flowing channels (four of seven sub-sites) rather than open lagoons, closed lagoons or backwaters. Group III sub-sites were associated with the Baía River (four of eleven sub-sites) and the Ivinheima River (five of eleven sub-sites) and with open lagoons (seven of 11 sub-sites). Group II sub-sites were associated with all three rivers and tended to be adjacent to open lagoons like group III.

Group I was characterised by more terrestrial vegetation than groups II or III as might be expected on the more permanent, elevated banks of river channels which characterised this group. Grasses were very frequent and abundant and creepers were also common.

Polygonum ferrugineum, *Polygonum* sp., *Cyperus* sp. and *Ludwigia* sp. all tended to be absent from group I sites. Several rarer species were confined to group I including *Scleria pterota* and *Andropogon bicornis*.

Polygonum sp. was very frequent and abundant in both groups II and III and *Ludwigia* sp. moderately abundant while Poaceae was occasional and creepers were very rare. Group II was characterised by the presence of *Cyperus* sp. together with *Sagittaria montevidensis*

and *Eichhornia azurea* which did not occur in the other groups. Most occurrences of *Fleocharis* sp. were in group II and *Polygonum ferrugineum* was also frequent. The common species in this group, and the presence of the aquatic species, *E. azurea*, suggest a wetter environment than group I, which could be expected on the low elevation temporary banks. Group III was similar to group II in some respects but *Cyperus* sp. was generally absent from sub-sites and *Polygonum stelligerum* was more frequent.

The contrasting characteristics of the TWINSpan groups are summarised in Table 3.38.

Table 3.38 Summary of contrasting 2001 B1 and B2 TWINSpan group characteristics.

TWINSpan group	I	II	III
Number of sites	7	11	11
Indicator species	Abundant Poaceae, moderately abundant creepers, <i>Inga</i> sp. present.	Cyperaceae present.	Cyperaceae absent.
Predominant river association	Paraná; flowing channels.	Paraná, Baía, Ivinheima; open lagoons.	Baía, Ivinheima; open lagoons.
Environmental characteristics	Low soil N and Ca, less open, more shaded.	Low soil N and Ca, more open, less shaded.	High soil N and Ca, more open, less shaded.
Vegetation characteristics	Tall, high biomass, intermediate cover.	Short, low biomass, low cover.	Tall, intermediate biomass, high cover.
Traits of dominant species	Long stems and small leaf area.	Short stems and large leaf area.	Intermediate stems and small leaf area.

Environmental comparisons

Soil nitrogen was much greater in group III than in groups I or II. Mean sub-site elevation was significantly lower in group II than in either of the other groups, suggesting a greater water availability at these sites which would account for the wetland species characterising this group. In general, soil phosphorus, calcium and iron were relatively similar in groups I and II and particularly high in group III but these differences were only close to significance in the case of calcium. In all three groups, most sub-sites had no evidence of grazing. Sub-sites were more shaded (mode = two, *i.e.*, slight shade) and less open (mode = three, *i.e.*, 50% of sky obscured by trees or shrubs) in group I than in groups II or III.

Table 3.39 Means, standard errors and significance of differences (one-way ANOVA) between 2001 B1 & B2 TWINSPAN groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Distance from water (m)	5.50	1.38	3.82	0.94	7.73	2.53	0.374
*Elevation above water (m)	1.50 ^a		0.20 ^b		0.70 ^a		<0.001
Soil pH	5.25	0.17	5.47	0.26	5.07	0.26	0.489
Soil ADAS ext. P (mgkg ⁻¹)	18.70	6.08	17.43	3.54	27.80	2.94	0.126
Soil total Kjeldahl N (mgkg ⁻¹)	2655 ^a	974	3280 ^a	1282	9988 ^b	2656	0.032
Soil total Fe (mgkg ⁻¹)	40028	7209	40928	6113	59006	7948	0.122
Soil total Ca (mgkg ⁻¹)	1032	208	1538	312	3684	842	0.054

Collective vegetation comparisons

The difference in plant communities between groups I, II and III was also shown by the significantly different biomass, canopy height and canopy cover of the vegetation (Table 3.40). Biomass and canopy height were significantly greater in group I than in group II but similar to group III. High biomass and canopy height in group III could be a result of the relatively high soil nitrogen and calcium concentrations associated with this group, although nutrient levels were not as high at group I sub-sites which shared these vegetation characteristics. Canopy cover in group I was not significantly different from either of the other two groups while group III had significantly greater canopy cover than group II.

Comparisons of traits of dominant species

As well as differing in species assemblage and collective vegetation structure, the TWINSPAN groups also differed significantly in the traits of the dominant species (Table 3.40). Leaf area was significantly greater in group II than in groups I or III and stem length was significantly greater in group I than in group II but similar to group III.

Table 3.40 Means, standard errors and significance of differences (t-tests) between 2001 B1 & B2 TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	9.86	1.94	12.27	1.67	7.36	1.11	0.075
Dry weight biomass (gm ⁻²)	549.14 ^a	184.86	167.45 ^b	32.19	501.94 ^a	69.00	0.001
Canopy height (m)	0.79 ^a	0.20	0.22 ^b	0.04	0.79 ^a	0.10	<0.001
Canopy cover (%)	56.11 ^{ab}	9.31	50.98 ^b	6.59	78.89 ^a	3.43	0.006
Stem density (m ⁻²)	492.1	72.32	444.44	207.49	373.7	56.52	0.444
Total leaf dry weight per plant (g)	1.69	0.54	4.41	3.30	3.34	0.43	0.188
Total leaf area per plant (cm ²)	246.63 ^a	80.94	549.37 ^b	258.23	471.05 ^a	68.98	<0.001
*Specific leaf area (cm ² g ⁻¹)	151.3		197.5		130.9		0.108
Remainder dry weight per plant (g)	2.72	0.74	2.89	2.25	4.44	0.75	0.057
Total plant dry weight (g)	4.48	1.23	7.56	5.65	7.90	1.15	0.070
Maximum stem length (m)	0.82 ^a	0.17	0.30 ^b	0.07	0.82 ^{ab}	0.09	0.025

TWINSpan analysis of 2000-2001 B2 bank data

Thirty-seven sub-sites were considered in the analysis of the two-year species data set collected from banks and shores. These consisted of the B sub-sites sampled in 2000 and the corresponding sub-sites sampled in 2001, B2 sub-sites. B1 sub-sites were not included because these were temporary environments which were not observed in 2000.

After correcting one misclassification, the first division gave a group of twelve sites (group I), indicated by abundant *Polygonum* sp., and a group of 25 sites (group II) in which *Polygonum* sp. was much less frequent and abundant. The eigenvalue for this division was 0.574. In the second division, group I was split into a group of eight sub-sites (group Ia), indicated by the presence of *Polygonum stelligerum* and *Commelina* sp., and a group of four sub-sites (group Ib), indicated by abundant *Polygonum* sp. and by the presence of creepers (eigenvalue = 0.440). Also at the second level of division, two sub-sites were split from group II due to the presence of *Polygonum acuminatum* (eigenvalue = 0.591) and then at the third division the remaining 22 sub-sites were split into a group of eight (group IIa), indicated by the presence of *Andropogon bicornis*, *Scleria pterota*, *Mimosa* sp. and ferns, and a group of fourteen (group IIb), indicated by very abundant Poaceae. As the eigenvalue dropped to 0.391 at this division, no further divisions were interpreted.

Comparisons of TWINSPAN groups

Site locations and species compositions

Group I was composed of sites in which *Polygonum* sp., *Polygonum stelligerum* and *Ludwigia* sp. tended to be important while grasses, creepers and ferns were more important in group II. This suggests a separation related to water availability with group I sub-sites being wetter than group II, although this was not supported by measurements of sub-site elevation above and distance from the water, which were similar between the two groups. All but one of the sub-sites in group I were located on gently sloping banks while the nine sub-sites located on steep banks all occurred in group II. The groups also differed in the river and the type of waterbody with which their sub-sites were associated. Two thirds of the sub-sites in group II were associated with the Paraná River compared with one third in group I. In group I, the sub-sites were divided equally between the Paraná, Baía and Ivinheima Rivers. Group II sub-sites were much more commonly associated with flowing channels (11 of 25) than group I which had only one sub-site associated with a flowing channel. Instead, group I sub-sites were predominantly associated with open lagoons and backwaters. These waterbody types were less common in group II. Closed lagoons (temporary or permanent) were more common in group II than in group I.

Groups Ia and Ib were quite similar in their associations with waterbody types and rivers. In both groups, sub-sites were associated with all three rivers and mainly with open lagoons, although group I also had two sites associated with backwaters, while group II had none. The separation of these two groups was shown in the TWINSPAN output table to be based on the particularly high abundance of *Polygonum* sp. in group IIa (although it was also very abundant in group Ia), the presence of creepers and the absence of *Commelina* sp.. The groups also differed in that group Ia supported a number of rare species which did not occur in group Ib. These factors led to a reasonably high eigenvalue but the differences in rare species do not provide reliable evidence of different communities as they may be absent from suitable growing sites by chance. Groups Ia and Ib therefore appear to be relatively similar in species assemblage and sub-site type.

Groups IIa and IIb differ more noticeably from each other. Most of the sub-sites in group IIb were associated with the Paraná River (eleven of fourteen) while those in group IIa were associated with all three rivers. However, the group IIa sub-sites were associated with a variety of waterbody types while all but one of group IIb sub-sites were associated with flowing channels. Furthermore, group IIa was composed mainly of sub-sites located on steep banks (six of eight) while those in group IIb were mostly located on gentle slopes

(eleven of fourteen). Group IIa was characterised by the presence of *Andropogon bicornis*, *Scleria pterota* and ferns, which were moderately rare but all occurrences were confined to this group. *Mimosa* sp., which was frequent across the B sub-sites but generally at low abundance, was more frequent in group IIa than IIb. Poaceae occurred across most group II sub-sites but was slightly more abundant in group IIb than group IIa.

The contrasting characteristics of the two main groups are summarised in Table 3.42 and those of the sub-groups in Table 3.41.

Table 3.41 Summary of contrasting 2000-2001 B TWINSPAN sub-group characteristics.

TWINSpan group	Ia	Ib	IIa	IIb
Number of sites	8	4	8	14
Indicator species	<i>Polygonum stelligerum</i> and <i>Commelina</i> sp. present.	Abundant <i>Polygonum</i> sp. and creepers.	<i>Andropogon bicornis</i> , <i>Scleria pterota</i> , <i>Mimosa</i> sp. and ferns present.	Abundant Poaceae.
Predominant river association	Paraná, Baía, Ivinheima; open lagoons.	Paraná, Baía, Ivinheima; open lagoons.	Paraná, Baía, Ivinheima; all waterbody types.	Paraná; flowing channels.
Bank type	Gentle slope.	Gentle slope.	Steep banks.	Gentle slopes.
Environmental characteristics	High soil P, N and Ca, open, unshaded.	High soil P, N and Ca, open, unshaded.	Low soil P, N and Ca, less open, more shaded.	High soil P, intermediate N, low Ca, less open, more shaded.
Vegetation characteristics	Low species richness.	Low species richness.	High species richness.	Low species richness.
Traits of dominant species	Similar			

Table 3.42 Summary of contrasting 2000-2001 B TWINSPAN group characteristics.

TWINSPAN group	I	II
Number of sites	12	25
Indicator species	Abundant <i>Polygonum</i> sp.	Less <i>Polygonum</i> sp.
Predominant river association	Paraná, Baía, Ivinheima; open lagoons and backwaters.	Paraná; flowing channels.
Bank type	Gentle slope.	Steep banks.
Environmental characteristics	High soil P, N and Ca, open, unshaded.	Low soil P, N and Ca, less open, more shaded.
Vegetation characteristics	High canopy cover.	Low canopy cover.
Traits of dominant species	Similar	

Environmental comparisons

Table 3.43 Means, standard errors and significance of differences (one-way ANOVA) between 2000-2001 B TWINSPAN groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group Ia		Group Ib		Group IIa		Group IIb		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Distance	6.63	3.40	6.00	1.35	2.81	0.41	4.68	1.25	0.230
*Elevation	0.35		0.75		1.00		0.50		>0.100
Soil pH	4.97	0.24	5.38	0.55	5.30	0.17	4.97	1.33	0.466
Soil ADAS	25.92 ^a	2.77	23.42 ^a	1.28	8.07 ^b	2.37	17.24 ^a	4.61	<0.001
ext. P (mgkg ⁻¹)									
Soil total	7491 ^a	3097	9367 ^a	4347	1566 ^b	796	2950 ^{ab}	789	0.011
Kjeldahl N (mgkg ⁻¹)									
Soil total Fe	59440	9254	52331	12670	36598	3834	41690	11142	0.082
(mgkg ⁻¹)									
Soil total Ca	2899	1128	3329	1157	909	247	1033	276	0.036
(mgkg ⁻¹)									

Soil phosphorus was significantly lower in group IIa than in any of the other three groups (Table 3.43). Soil nitrogen was also particularly low in this group and significantly lower than in group Ia or Ib (Table 3.43). Soil calcium was lowest in group IIa, slightly higher in group IIb and markedly higher in groups Ia and Ib (Table 3.43). Soil pH, soil iron and distance of the sub-sites from water did not differ significantly between groups. In all four

TWINSpan groups, most sub-sites had no evidence of grazing. Groups IIa and IIb included more shaded sub-sites (scores two, three or four) than groups Ia and Ib in which all sub-sites were completely unshaded (score one). Group IIa and IIb sub-sites were also correspondingly less open (mode = three in both groups) than groups Ia and Ib (mode = 1 in both groups).

Table 3.44 Means, standard errors and significance of differences (t-tests) between 2000-2001 B TWINSpan groups of normally distributed environmental variables (data back-transformed as necessary to give original values). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Distance	6.42	2.25	4.72	0.78	0.465
*Elevation	0.60		0.50		0.794
Soil pH	5.10	0.23	5.08	0.10	0.896
Soil ADAS ext. P (mgkg ⁻¹)	25.09	1.88	15.4	2.60	0.002
Soil total Kjeldahl N (mgkg ⁻¹)	8116	2421	3110	775	0.024
Soil total Fe (mgkg ⁻¹)	57070	7207	14001	2800	0.061
Soil total Ca (mgkg ⁻¹)	3043	816	1175	199	0.014

Soil phosphorus, soil nitrogen and soil calcium were significantly greater in group I than in group II (Table 3.44) and sub-sites were more open and less shaded.

Collective vegetation comparisons

Between the smaller TWINSpan groups, the mean number of species recorded at sub-sites was significantly greater in group IIa than in any of the other groups (Table 3.45).

The two large TWINSpan groups differed only in percentage canopy cover which was significantly greater in group I than in group II sub-sites (Table 3.46).

Table 3.45 Means, standard errors and significance of differences (one-way ANOVA) between 2000-2001 B TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group Ia		Group Ib		Group IIa		Group IIb		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	9.38 ^a	1.44	6.00 ^a	0.41	16.13 ^b	1.65	7.50 ^a	2.00	<0.001
Dry weight biomass (gm ⁻²)	400.87	90.95	423.89	23.36	491.02	114.17	886.78	237.00	0.277
Canopy height (m)	0.71	0.13	0.82	0.14	0.95	0.17	0.98	0.26	0.545
Canopy cover (%)	74.51	5.91	79.99	1.92	69.74	9.18	54.65	14.61	0.143
Stem density (m ⁻²)	443.06	71.62	313.89	28.46	791.67	173.03	688.89	184.11	0.201
Total leaf dry weight per plant (g)	2.81	0.52	3.88	0.52	5.17	2.19	2.63	0.70	0.491
*Total leaf area per plant (cm ²)	413.4		522.4		300.6		316.7		0.886
*Specific leaf area (cm ² g ⁻¹)	161.7		119.7		133.5		145.2		0.385
*Remainder dry weight per plant (g)	3.01		5.87		3.80		7.68		0.559
Total plant dry weight (g)	7.29	1.28	9.74	0.42	11.27	3.97	12.31	3.29	0.931
Maximum stem length (m)	0.73	12.72	0.10	28.79	1.16	21.85	1.19	4.71	0.228

Comparisons of traits of dominant species

The mean values of dominant species traits did not differ significantly between TWINSpan groups whether the larger (Table 3.46) or smaller groups (Table 3.45) were considered.

Table 3.46 Means, standard errors and significance of differences (t-tests) between 2000-2001 B TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	8.25	1.06	10.16	1.04	0.262
Dry weight biomass (gm ⁻²)	407.15	62.43	720.76	116.41	0.191
Canopy height (m)	0.74	0.10	0.91	0.10	0.299
Canopy cover (%)	76.34	3.97	61.48	5.26	0.031
Stem density (m ⁻²)	400.00	50.86	767.11	139.00	0.088
Total leaf dry weight per plant (g)	3.16	0.40	3.37	0.78	0.407
Total leaf area per plant (cm ²)	464.14	70.21	474.50	112.16	0.467
*Specific leaf area (cm ² g ⁻¹)	137.4		143.4		0.893
*Remainder dry weight per plant (g)	4.72		5.73		0.673
Total plant dry weight (g)	8.11	0.91	11.43	2.24	0.792
Maximum stem length (m)	0.80	0.09	1.13	0.11	0.074

TWINSpan analysis of 2002 bank data

In 2002, many more of the plants encountered during the surveys of bank and floodplain vegetation were identified to species level. Because of the absence of flowers, some samples could only be identified to genus or family level (and a few remained unidentified) but in general there was much greater taxonomic resolution in the data sets from 2002. The thirteen sites provided rather a small sample size but TWINSpan analysis was applied to find out if any vegetation communities could be suggested from the data.

Approximately one third of the species shown in the TWINSpan output table occurred at only one site (17 of 52), making it difficult to suggest community types with so many rare species. At the first level of division, two sites (group I) were separated from the rest because they supported abundant *Polygonum stelligerum* which was absent from the other sites. The eigenvalue for this division was 0.737. Two further sites were separated in the second division (group II) with an eigenvalue of 0.672. These two sites were indicated by the presence of *Iseia luxurians* which was absent from all other sites. In the third division, the remaining nine sites were split into a group of four (group IV), indicated by the presence of unidentified herbaceous plants and a group of five (group III), in which these were present only once at low abundance. The eigenvalue for this division was 0.650.

Comparisons of TWINSPAN groups

Site locations and species compositions

The groups resulting from TWINSPAN analysis were very small, making it more difficult to identify patterns in their composition. However, all of the sub-sites in group IV were associated with the Paraná River and three out of four of these were closed, temporary lagoons on islands. This group had more unidentified herbaceous plants than the others, but this division may be due to the problems of identification because a number of herbaceous dicots were identified to genus or species in group III. Group III had sub-sites from the Baía and Paraná Rivers and the Curutuba channel and three out of five were associated with flowing channels. *Ludwigia* sp., *Commelina* sp., Cyperaceae, grasses and woody species were more common in this group than the others. Both of the sites in group I were associated with the Ivinheima River and had very abundant *Polygonum stelligerum*.

The contrasting characteristics of the four TWINSPAN groups are summarised in Table 3.47.

Table 3.47 Summary of contrasting 2002 B TWINSPAN group characteristics.

TWINSPAN group	I	II	III	IV
Number of sites	2	1	5	4
Indicator species	Abundant <i>Polygonum stelligerum</i> .	<i>Iseia luxurians</i> present.	None	Abundant herbaceous dicotyledonous plants.
Predominant river association	Ivinheima; lagoons.	Ivinheima; channel.	Baía, Paraná; flowing channels.	Paraná; temporary lagoons.
Bank type	Gentle slopes.	Gentle slope.	Steep banks.	Gentle slopes.
Environmental characteristics	Lower mean soil P, high mean soil N, open, unshaded.	Lower soil P & N, less open.	Higher mean soil P, low mean soil N, less open, more shaded.	Higher mean soil P, low mean soil N, less open, more shaded.
Vegetation characteristics			More species rich.	Less species rich.
Traits of dominant species	Generally larger plants.	Relatively large plant.	Generally smaller plants.	Generally smaller plants.

Environmental comparisons

Table 3.48 Means (and standard errors for larger groups) of 2002 B TWINSPAN groups of normally distributed environmental variables (data back-transformed as necessary to give original values). P-values indicate significance of differences between groups III and IV (t-tests).

Variable	Group I	Group II	Group III		Group IV		p
	Mean	Mean	Mean	S.e.	Mean	S.e.	
Distance from water (m)	2.65	2.90	2.00	0.65	2.88	1.39	0.597
Elevation above water (m)	0.35	1.35	0.42	0.16	0.48	0.18	0.804
Soil pH	5.17	4.58	5.11	0.11	4.85	0.24	0.363
Soil ADAS ext. P (mgkg ⁻¹)	8.35	11.32	21.82	10.15	19.94	4.80	0.755
Soil total Kjeldahl N (mgkg ⁻¹)	6275	2820	3044	944.16	2775	724.22	0.873
Soil total Fe (mgkg ⁻¹)	63900	53000	27060	3335	31650	1779	0.210
Soil total Ca (mgkg ⁻¹)	2065	1131	656	170	1132	218	0.135

Table 3.48 shows the values of the environmental variables for each site, or the mean value for each group of sites, separated by TWINSPAN analysis. Soil nitrogen and calcium were much higher in group I than in the other groups. Calcium was particularly low in group III. Soil iron was much higher in groups I and II than in groups III and IV. Soil phosphorus was much lower in groups I and II than in groups III and IV. Soil pH was lowest in group II and highest in group I. Elevation was much greater in group II than in any of the other groups. Distance was similar between groups but a little smaller in group III than in the other groups. Only one sub-site had any evidence of grazing (RPM3 in group III) and so grazing pressure did not differ between groups. Group I sub-sites were both completely open and unshaded, while groups II, III and IV included sub-sites of varying open-ness and shading.

None of the environmental variables was significantly different between the two larger groups (Table 3.48).

Collective vegetation comparisons

Table 3.49 shows the value of the collective vegetation and dominant species trait variables measured at each sub-site, or the mean value for each group of sub-sites, split off by TWINSPAN analysis. Groups III and IV had higher mean species richness than groups I and II. Group III was significantly higher than group IV. Biomass was greatest in group II, lower in group I and much lower than both of these groups in groups III and IV. Groups II and III had similar canopy height which was shorter than groups I and IV.

Canopy cover was similar in all groups but a little lower in group III. Stem density was similar and low in groups I and III. It was intermediate in group II and much higher in group IV.

Species richness was the only variable which differed significantly between the two larger groups, being greater in group III than group IV.

Table 3.49 Means (and standard errors for larger groups) of 2002 B TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). P-values indicate significance of differences between groups III and IV (t-tests).

Variable	Group I	Group II	Group III		Group IV		p
	Mean	Mean	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	6.50	7.00	15.40	1.50	9.25	1.18	0.015
Dry weight biomass (gm ⁻²)	1144.67	2116.08	408.21	137.25	544.44	93.72	0.298
Canopy height (m)	1.14	0.61	0.68	0.18	0.96	0.20	0.245
Canopy cover (%)	92.22	95.56	72.44	10.35	94.17	3.38	0.105
Stem density (m ⁻²)	611.11	1512.5	526.67	85.10	2227.08	1286.68	0.157
Total leaf dry weight per plant (g)	2.80	2.19	0.49	0.22	0.90	0.23	0.236
Total leaf area per plant (cm ²)	375.29	328.34	86.26	30.62	165.77	47.39	0.214
Specific leaf area (cm ² g ⁻¹)	134.39	164.27	208.37	40.98	186.19	18.78	0.642
Remainder dwt per plant (g)	18.20	9.48	1.87	1.20	3.83	1.08	0.167
Total plant dry weight (g)	20.99	11.67	2.36	1.42	4.73	1.30	0.154
Maximum stem length (m)	1.62	1.24	0.69	0.23	1.03	0.27	0.199

Comparisons of traits of dominant species

Total leaf weight, leaf area, remainder weight and total plant weight were lowest in group III, stem length was shortest and SLA was greatest. Group I had greatest leaf weight, leaf area, remainder weight, total plant weight and stem length and lowest SLA.

None of the dominant species trait variables differed significantly between the two larger groups (Table 3.49).

3.4.3 Identification of floodplain vegetation communities

TWINSPAN analysis of 2000 floodplain data

Nineteen floodplain (C) sub-sites were sampled in 2000. The first division in TWINSPAN analysis of these sites produced two groups, one of fifteen (group I), indicated by the presence of unidentified creepers and herbaceous dicotyledonous plants, and one of five (group II), indicated by abundant unidentified woody plants and by the presence of *Ludwigia* sp. and *Sida* sp.. The TWINSPAN output showed that one site, LOS, had been misclassified in group II and so it was transferred to group I before comparisons were made between the groups. The eigenvalue for this division was 0.477. In the second division, two sites were split from group I indicated by the presence of *Conyza* sp. which was not recorded at any other sites. In the third level of division, three more sites were split off, indicated by the presence of *Crotalaria* sp., woody plants and abundant Poaceae. The remaining nine sites were indicated by the presence of creepers, Cyperaceae, unidentified herbaceous dicotyledonous plants and *Mimosa* sp.. The eigenvalue for this division was 0.411. As only small groups were produced by further divisions, the analysis was stopped at this stage and comparisons were made between group I and group II which resulted from the first division.

Comparisons of TWINSPAN groups

Site locations and species compositions

TWINSPAN groups I and II were very different in species assemblage, sharing only five taxa out of the 35 recorded across all of the sites. These were Poaceae, which was frequent and abundant across both groups, *Lippia alba*, which occurred once in each group, and the categories of woody plants, seedlings and unidentified herbaceous plants. Unidentified herbaceous plants were more common in group I and so were used as an indicator species. Many rarely recorded taxa were confined to group I. Some of the less rare species and plant groups were *Eupatorium pauciflorum*, *Aspilia latissima*, *Mimosa* sp, Cyperaceae and creepers. Although woody plants were identified as an indicator of group II, the transfer of LOS to group I when it was found to be misclassified meant that abundant woody plants were no longer limited to group I sites. The strong effect of this single site is due to the small sample size. This highlights the need for the larger data set provided by combining the data collected over two years of sampling. All of the species restricted to group II were very rare with only one or two occurrences. These included *Ludwigia* sp. and *Sida* sp..

Table 3.50 summarises the characteristics which contrasted between the TWINSPAN groups.

Table 3.50 Summary of contrasting 2000 C TWINSPAN group characteristics.

TWINSPAN group	I	II
Number of sites	15	5
Indicator species	Presence of creepers and herbaceous plants.	Presence of <i>Ludwigia</i> sp. and <i>Sida</i> sp., abundant woody plants.
Predominant river association	Paraná and Baía	Paraná
Environmental characteristics	Low soil Fe.	High soil Fe.
Vegetation characteristics	Similar	
Traits of dominant species	Long stems.	Short stems.

Neither of the TWINSPAN groups was associated with a particular river or waterbody type.

Environmental comparisons

Mean soil iron was significantly greater in group II than in group I (Table 3.51). It was difficult to draw conclusions from comparisons of the grazing, shade and open-ness scores between the two groups because of the very different sizes of the groups. However, a greater proportion of group II sites than group I sub-sites showed evidence of intense grazing (scores of four or five). Most sub-sites in both groups were relatively open and unshaded. None of the other environmental variables differed significantly between the TWINSPAN groups.

Table 3.51 Means, standard errors and significance of differences (t-tests) between 2000 C TWINSPAN groups of normally distributed environmental variables (data back-transformed as necessary to give original values).

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Distance from water (m)	26.07	6.21	67.50	45.21	0.579
Elevation above water (m)	2.14	0.27	2.13	0.63	0.983
Soil pH	5.01	0.23	4.75	0.60	0.520
Soil ADAS ext. P (mgkg ⁻¹)	16.04	3.32	17.55	7.81	0.802
Soil total Kjeldahl N (mgkg ⁻¹)	2642	403	3080	857	0.668
Soil total Fe (mgkg ⁻¹)	37847	4234	52625	3643	0.023
Soil total Ca (mgkg ⁻¹)	1011	145	1080	362	0.959

Collective vegetation comparisons

None of the collective vegetation variables differed significantly between the TWINSpan groups (Table 3.52).

Comparisons of traits of dominant species

There were contrasts in dominant species trait variables between the TWINSpan groups. Total leaf area and maximum stem length were significantly greater in group I than in group II (Table 3.52).

Table 3.52 Means, standard errors and significance of differences (t-tests) between 2000 C TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values).

Variable	Group I		Group II		p
	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	9.93	1.39	9.50	0.87	0.791
Dry weight biomass (gm^{-2})	520.44	128.99	336.05	68.58	0.913
Canopy height (m)	0.71	0.16	0.29	0.10	0.304
Canopy cover (%)	70.50	7.28	72.17	14.25	0.922
Stem density (m^{-2})	831.11	171.62	702.78	268.03	0.703
Total leaf dry weight per plant (g)	5.29	1.77	0.38	0.22	0.065
Total leaf area per plant (cm^2)	767.74	251.75	50.56	18.24	0.017
Specific leaf area (cm^2g^{-1})	226.78	33.65	206.90	43.84	0.730
Remainder dry weight per plant (g)	6.99	2.00	0.87	0.40	0.085
Total plant dry weight (g)	12.99	3.51	1.59	0.63	0.083
Maximum stem length (m)	1.00	0.20	0.44	0.12	0.025

TWINSpan analysis of 2001 floodplain data

Eigenvalues were very high (all over 0.5) in the TWINSpan analysis of the 2001 C species data indicating strongly differing species assemblages. Twenty C sub-sites were sampled in 2001. The first level of division separated these into a group of five (group I), indicated by the presence of *Polygonum* sp. and *Polygonum stelligerum*, and a group of fifteen, indicated by the presence of unidentified woody plants and by moderately abundant Poaceae. In the second division, two sites were lost from the group of fifteen. The indicator species for this pair of sub-sites was *Scleria pterota* and the eigenvalue for the division was 0.596. The remaining thirteen sites were then divided into a group of six sites (group II), indicated by the presence of unidentified woody plants, and a group of

seven sites (group III) from which woody plants tended to be absent. The eigenvalue was 0.556. The eigenvalues of further divisions were still high but the resulting groups were very small.

Comparisons of TWINSpan groups

Site locations and species compositions

Four of the five sub-sites in group I were associated with the Ivinheima River while group II sub-sites tended to be associated with the Paraná River (four of six) and group III sub-sites were located near all three rivers. Group III sub-sites were also associated with a variety of waterbody types (channels, open lagoons and closed lagoons). Group I sub-sites were mostly associated with open lagoons (four of five) and group II sub-sites with flowing channels (three of six) and backwaters (two of six). The groupings were not related to whether or not there was grazing or a tree canopy at the sub-sites.

Poaceae and creepers were common across the data set, occurring at fourteen and ten out of twenty sites respectively. Group I was characterised by a general absence of Poaceae and woody plants and by the presence of *Polygonum stelligerum* and *Polygonum* sp.. Some rarer species were also confined to this group. Group II included most of the sub-sites at which woody plants were recorded and was associated with abundant Poaceae while *Polygonum* species were absent. Group III had very high abundance of Poaceae at all sub-sites. *Polygonum* sp. and woody plants tended to be absent and some other taxa rarer in the data set, such as Cyperaceae, were confined to this group.

The contrasting characteristics of the TWINSpan groups are summarised in Table 3.53.

Table 3.53 Summary of contrasting 2001 C TWINSPAN group characteristics.

TWINSPAN group	I	II	III
Number of sites	5	6	7
Indicator species	Presence of <i>Polygonum</i> sp. and <i>P. stelligerum</i> .	Presence of woody plants.	None
Predominant river association	Ivinheima; open lagoons.	Paraná; flowing channels and backwaters.	Paraná, Baía, Ivinheima; all waterbody types.
Environmental characteristics	More acidic soil pH, high soil P, N and Ca, minimal grazing, open, unshaded.	Less acidic soil pH, low soil P, N and Ca, grazed, less open, more shaded.	More acidic soil pH, low soil P, N and Ca, ungrazed.
Vegetation characteristics	Similar.		
Traits of dominant species	Large leaf area.	Small leaf area.	Small leaf area.

Environmental comparisons

Table 3.54 Means, standard errors and significance of differences (one-way ANOVA) between 2001 C TWINSPAN groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons).

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Distance (m)	11.20	2.24	18.33	2.11	17.14	6.35	0.366
Elevation (m)	1.24	0.17	2.12	0.64	1.21	0.23	0.355
Soil pH	4.24 ^a	0.06	5.10 ^b	0.29	4.85 ^a	0.10	0.013
Soil ADAS ext. P (mgkg ⁻¹)	44.39 ^a	7.83	17.88 ^b	2.97	21.01 ^b	4.31	0.007
Soil total Kjeldahl N (mgkg ⁻¹)	18136 ^a	4470	2183 ^b	398	3413 ^b	1194	<0.001
Soil total Fe (mgkg ⁻¹)	60337	9569	38636	7616	33866	5541	0.072
Soil total Ca (mgkg ⁻¹)	4430 ^a	1346	1032 ^b	266	952 ^b	154	0.002

There were significant differences between TWINSPAN groups in soil pH, soil phosphorus, soil nitrogen and soil calcium (Table 3.54). Soil pH was significantly less acidic in group II than in groups I and III. Group I had significantly greater soil phosphorus, soil nitrogen and soil calcium than either group II or group III. Values for these variables were relatively similar between groups II and III. There was not a significant difference in soil iron between groups, but the mean values followed the same pattern as phosphorus, nitrogen and calcium. The pattern of grazing, open-ness and shade scores differed between the three groups. All sub-sites in group III were ungrazed and

only one sub-site in group I showed evidence of grazing (score two, *i.e.*, evidence of light grazing), while only one sub-site in group II was ungrazed. Sub-sites in group I were open (scoring one or two) and unshaded, while those in group II tended to be less open with some shade. Group III included some sub-sites that were completely open and unshaded (scoring one on both scales) and others that were deeply shaded (scoring four) with a large proportion of the sky obscured by surrounding vegetation (scoring four or five).

Collective vegetation comparisons

None of the collective vegetation variables differed significantly between the TWINSpan groups (Table 3.55).

Table 3.55 Means, standard errors and significance of differences (one-way ANOVA) between 2001 C TWINSpan groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		Group III		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Number of species (per sub-site)	4.40	1.29	8.83	1.40	6.43	0.92	0.070
Dry weight biomass (gm ⁻²)	554.64	142.28	600.42	188.41	738.04	206.15	0.740
Canopy height (m)	0.78	0.20	0.69	0.18	1.02	0.18	0.443
Canopy cover (%)	63.33	14.83	56.94	12.20	51.03	10.85	0.789
Stem density (m ⁻²)	288.9	56.33	375.93	64.50	436.51	73.09	0.341
Total leaf dry weight per plant (g)	2.23	0.40	1.64	0.56	2.77	1.13	0.556
Total leaf area per plant (cm ²)	562.01 ^a	81.40	257.98 ^b	34.64	449.43 ^b	168.69	0.054
*Specific leaf area (cm ² g ⁻¹)	207.7		151.9		156.0		0.511
Remainder dry weight per plant (g)	3.61	0.82	4.96	2.56	5.17	2.23	>0.999
Total plant dry weight (g)	5.83	1.21	6.60	2.52	7.94	3.31	0.992
Maximum stem length (m)	91.40	0.16	99.50	0.15	94.21	0.13	0.925

Comparisons of traits of dominant species

Total leaf area was the only trait that differed significantly between TWINSpan groups (Table 3.55). It was significantly greater in group I than in group II or group III.

TWINSPAN analysis of 2000-2001 floodplain data

Combining all of the C sub-sites surveyed during 2000 and 2001 gave a total of 39 sub-sites. In the first division of TWINSPAN analysis, four sites were split from the main group indicated by the presence of *Polygonum* sp. and by abundant *P. stelligerum* (group I). The eigenvalue for this division was 0.640. The main group of 35 sites was indicated by the presence of creepers and moderately abundant Poaceae. In the second division, this group was split into a group of seven sub-sites (group II), indicated by the presence of *Conyza* sp. and by moderately abundant creepers, and a group of 28 sub-sites, indicated by moderately abundant Poaceae. The eigenvalue for this division was 0.444. In the third division (eigenvalue = 0.390), the 28 sub-sites were split into a group of seven sub-sites (group III), indicated by the presence of *Ludwigia* sp., and a group of 21 sub-sites, indicated by the presence of creepers and unidentified woody plants and herbaceous dicotyledonous plants. The next division had an eigenvalue of 0.353 and split the remaining 21 sub-sites into a group of nine (group IV), indicated by the presence of *Mimosa* sp. and Cyperaceae and by moderately abundant creepers and abundant unidentified herbaceous plants, and a group of twelve (group V) indicated by the presence of *Galeanthe brasiliensis* and by moderately abundant unidentified woody plants. One of the sites in group IV had been misclassified and so was transferred into group V.

Comparisons of TWINSPAN groups

Site locations and species compositions

TWINSPAN analysis broke down a large number of sites into smaller groups with gradually decreasing eigenvalues. The first division had a particularly high eigenvalue indicating that group I had a very different species assemblage from the remaining sub-sites. The sub-sites in this group supported a small number of species and all four were strongly dominated by *Polygonum* species. Poaceae was not important in this group. Creepers were important in group II and Poaceae was still uncommon. This group also supported a number of plants which were rarely recorded during the surveys, for example *Sapium longifolium*, *Palicourea crocea*, *Eupatorium laevigatum* and ferns. Group III was dominated by Poaceae and was also associated with *Ludwigia* sp.. There were no unidentified herbaceous plants or woody plants in this group. Group IV sub-sites were dominated by Poaceae but creepers were also important. In group V, Poaceae tended to be dominant but creepers were much less abundant. Unidentified herbaceous plants and woody plants were also common in this group.

Group I sub-sites were associated with the Ivinheima River and with open lagoons. None of the sub-sites in this group was wooded or had any evidence of grazing. Group V sub-sites tended to be associated with the Paraná River and evidence of grazing was observed more frequently than in the other groups. In groups II and III, there were sub-sites associated with all three rivers and a mixture of waterbody types. Both groups had wooded and unwooded and grazed and ungrazed sub-sites. Group IV was associated with the Paraná and Baía Rivers and with flowing channels.

The contrasting characteristics of the TWINSPAN groups are summarised in Table 3.56.

Table 3.56 Summary of contrasting 2000-2001 C TWINSPAN group characteristics.

TWINSPAN group	I	II	III	IV	V
Number of sites	4	7	7	8	13
Indicator species	Presence of <i>Polygonum</i> sp., abundant <i>P. stelligerum</i> .	Presence of <i>Conyza</i> sp., moderately abundant creepers.	Presence of <i>Ludwigia</i> .	Presence of <i>Mimosa</i> sp. and Cyperaceae, moderately abundant creepers, herbaceous plants.	Presence of <i>Galeanthe brasiliense</i> , moderately abundant woody plants.
Predominant river association	Ivinheima; open lagoons.	Paraná, Baía, Ivinheima, all waterbody types.	Paraná, Baía, Ivinheima, all waterbody types.	Paraná, Baía; flowing channels.	Paraná
Environmental characteristics	High soil N and Ca, ungrazed, open, unshaded.	Low soil N and Ca, ungrazed, mostly unshaded.	Low soil N and Ca, ungrazed, mostly unshaded.	Low soil N and Ca, ungrazed, mostly unshaded.	Low soil N and Ca, grazed, mostly unshaded.
Vegetation characteristics	Low species richness.	High species richness.	High species richness.	High species richness.	High species richness.
Traits of dominant species	Similar.				

Environmental comparisons

Soil nitrogen and calcium were significantly greater in group I than in any of the other groups (Table 3.57). Mean soil phosphorus and iron were also greatest in group I but there were no significant differences between groups. In groups I, II, III and IV, most sites were ungrazed, but in group V, although the most frequent grazing score was one (no evidence

of grazing), most sub-sites showed some signs of grazing and scored between two and five (minimal to severe grazing). All sub-sites in group I were unshaded and only one site was not completely open. Most sub-sites in each of the other groups were also unshaded but varied in open-ness within the groups.

Table 3.57 Means, standard errors and significance of differences (one-way ANOVA) between 2000-2001 C TWINSpan groups of normally distributed environmental variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons).

Variable	Group I		Group II		Group III		Group IV		Group V		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
Distance (m)	12.00	2.71	14.43	2.95	18.43	6.20	17.38	5.14	42.08	14.80	0.147
Elevation (m)	1.18	0.20	2.11	0.52	1.61	0.44	1.81	0.34	1.85	0.31	0.768
Soil pH	4.23	0.08	4.94	0.29	5.07	0.29	4.80	0.35	4.87	0.13	0.312
Soil ADAS ext. P (mgkg ⁻¹)	42.48	9.80	28.54	6.89	19.24	6.05	18.60	5.32	14.68	2.17	0.130
Soil total Kjeldahl N (mgkg ⁻¹)	20121 ^a	5170	3501 ^b	1238	2876 ^b	759	3215 ^b	961	2360 ^b	362	0.001
Soil tot. Fe (mgkg ⁻¹)	58188	12038	42199	8427	40328	7490	40799	4511	38028	4115	0.403
Soil tot. Ca (mgkg ⁻¹)	5123 ^a	1490	1223 ^b	247	1077 ^b	313	933 ^b	123	939 ^b	122	<0.001

Collective vegetation comparisons

Species richness was significantly lower in group I than in groups II, IV or V. Groups II and IV had highest species richness. Group I included the fewest number of sub-sites and so fewer species could be expected. None of the other collective vegetation variables differed significantly between groups.

Comparisons of traits of dominant species

There were no significant differences in dominant species trait variables between 2000-2001 TWINSpan groups.

Table 3.58 Means, standard errors and significance of differences (one-way ANOVA) between 2000-2001 C TWINSPAN groups of normally distributed collective vegetation and dominant species trait variables (data back-transformed as necessary to give original values). Contrasting superscript letters between groups indicate significant differences (Tukey's multiple comparisons). *Medians are quoted for non-normal variables compared using Kruskal Wallis tests.

Variable	Group I		Group II		Group III		Group IV		Group V		p
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	
No. species (per sub-site)	3.50 ^a	1.19	10.29 ^b	1.21	6.86 ^{ab}	1.03	10.63 ^b	2.14	7.83 ^b	0.90	0.002
Dwt biomass (gm ⁻²)	567.6	182.9	401.3	101.1	604.9	242.5	596.3	180.8	495.5	118.5	0.971
Canopy height (m)	0.79	0.26	0.74	0.17	0.87	0.23	0.64	0.17	0.61	0.17	0.939
Canopy cover (%)	60.42	18.77	64.76	8.52	46.37	8.37	65.10	11.14	69.94	8.59	0.461
Stem density (m ⁻²)	283.3	72.4	320.6	38.6	387.3	87.9	777.8	228.0	811.1	163.8	0.111
Total leaf dwt/plant (g)	2.22	0.52	3.16	1.20	2.42	2.21	6.09	2.93	2.09	0.99	0.826
*Leaf area (cm ²)	508.7		317.0		208.7		380.4		210.3		0.115
SLA (cm ² g ⁻¹)	439.7	262.8	170.7	24.7	194.4	34.4	257.5	69.8	253.7	52.1	0.740
*Remainder dwt/plant (g)	4.65		3.61		3.74		4.10		1.59		0.801
*Total dwt/plant (g)	7.43		6.08		5.28		6.16		3.40		0.833
Stem length (m)	0.90	0.20	0.89	0.10	0.89	0.15	1.01	0.30	0.87	0.17	0.989

TWINSpan analysis of 2002 floodplain data

Thirteen C sub-sites were surveyed in 2002 giving a species data set that was too small for TWINSpan analysis, considering the high proportion of species with few occurrences.

However, this data set was particularly interesting because the species list was much more detailed than in the previous two years and so it was investigated using the same methods.

During the analysis, sub-sites were gradually split off in small groups. The first division had an eigenvalue of 0.852 and separated one site from the rest, RPM3, which was indicated by the presence of *Garcynia gardneriana* but also had three other taxa which did not occur at any other site (the grass *Oplismenus hirtellus* and two woody plants *Psychotria leiocarpa* and a member of the Elaeocarpaceae). Eigenvalues were particularly high because very few species occurred at more than one of the thirteen sub-sites,

illustrating the high species diversity encountered during the surveys. The second division had an eigenvalue of 0.807 and separated three sites from the main group indicated by the presence of Convolvulaceae. Several other species were also exclusive to this group but most occurred at only one of the three sub-sites. Poaceae was abundant at most of the remaining sites. The third division separated two sites which supported *Ipomoea rubens* from the remaining group of 7. The eigenvalue for this division was 0.723. The last division had an eigenvalue of 0.545 and split the sub-sites into a group of three in which *Paspalum conspersum* was abundant, and a group of four from which this species was absent.

3.4.4 Correlation and regression analysis of bank and floodplain survey data: Investigating relationships between environmental, collective vegetation and dominant species trait variables

2000 Bank

Statistically significant ($p \leq 0.05$) Pearson product-moment correlation coefficients and regression equations describing relationships between pairs of vegetation, environment and trait variables are shown in Tables 3.59 and 3.60 respectively.

Species richness was related to one visually-assessed and three measured environmental variables and one dominant species trait variable (Table 3.59). The single best predictor was \log_e distance from water, which explained 33.2% of the variation in species richness (Table 3.60). In a quadratic relationship, species richness quickly declined at first with \log_e distance from water, then more slowly, and at the greatest distances very slightly increased. Multiple regression analysis showed that an even greater amount of variation in species richness could be explained by combining the predictor variables \log_e soil phosphorus and \log_e root weight (Equation 3.1).

Equation 3.1

$$\text{Species} = 17.5 - 2.95 \log_e \text{SP} + 1.54 \log_e \text{rwt}$$

$$r = 0.766, \text{ adjusted } r^2 = 0.523, p = 0.003.$$

Table 3.59 Significant ($p \leq 0.05$) Pearson product-moment correlation coefficients (r) between variables measured at bank sub-sites in 2000.

Variable 1	Variable 2	r	p
Species	\log_e Distance	-0.537	0.018
	\log_e SP	-0.569	0.011
	\log_e SN	-0.510	0.026
	Shade	+0.566	0.012
	\log_e rwt	+0.565	0.023
\log_e Biomass	\log_e twt	+0.475	0.040
	Cover	+0.460	0.048
Height	\log_e lwt	+0.628	0.004
	\log_e lar	+0.530	0.020
	$\sqrt{\text{rem}}$	+0.497	0.030
	\log_e twt	+0.634	0.004
Cover	\log_e Stem	+0.729	<0.001
	\log_e elevation	+0.477	0.039
	\log_e lwt	+0.646	0.003
	\log_e lar	+0.462	0.046
	\log_e rwt	+0.553	0.026
	$\sqrt{\text{rem}}$	+0.454	0.051
	\log_e twt	+0.580	0.009
\log_e Stem	\log_e Elevation	+0.483	0.036
	\log_e rwt	+0.553	0.026

Soil phosphorus and soil nitrogen were also good predictors of species richness accounting for 32.3% and 26% of variation respectively.

\log_e biomass was not significantly related to any of the environmental variables but was positively correlated with percentage canopy cover and with \log_e total plant weight, both of which explained a similar amount of variation (21.2% and 22.5%) (Table 3.60).

Combining the two variables did not explain any more variation.

Canopy height was significantly correlated with the dominant species trait variables \log_e leaf weight, \log_e leaf area, \log_e total weight and $\sqrt{\text{remainder weight}}$ (Table 3.59).

Regression analysis showed that the relationship with $\sqrt{\text{remainder weight}}$ was strongly influenced by one site, PR, where remainder weight was extremely high. As the relationship was dependent on this single site, it was not considered any further. \log_e total plant weight provided a more robust predictor of canopy height, explaining 40.2% of variation. An environmental predictor, \log_e soil phosphorus, was also found during

regression analysis. Canopy height showed a cubic response to soil phosphorus, increasing at first at low soil phosphorus then peaking and decreasing at intermediate soil phosphorus before increasing again at high soil phosphorus.

Canopy cover was significantly related to many variables (Table 3.60). The best single predictor of canopy cover was \log_e stem density which explained 53.1% of the variation. The relationship with $\sqrt{\text{remainder weight}}$ was not described as it was dependent on one outlying site, PR. However, there were significant positive linear relationships with \log_e leaf weight, \log_e root weight and \log_e total weight. The best of these was \log_e leaf weight which explained 41.8% of the variation. The environmental variables \log_e elevation and \log_e soil nitrogen were also related to canopy cover. Canopy cover initially increased at low levels of soil nitrogen then peaked and started to decrease at high levels. Cover increased linearly with elevation. The prediction of cover by environmental variables was improved by combining elevation and soil nitrogen in a multiple regression equation (Equation 3.2).

Equation 3.2

$$\text{Cover} = -892 + 40.8 \log_e \text{Elevation} + 245 \log_e \text{SN} - 15.9 \log_e \text{SN}^2$$

$$r = 0.767, \text{adjusted } r^2 = 0.506, p = 0.003.$$

Applying multiple regression analysis to all of the significant predictors increased the amount of variation explained to 65.5% (Equation 3.3).

Equation 3.3

$$\text{Cover} = -756 + 183 \log_e \text{SN} - 11.9 \log_e \text{SN}^2 + 20.0 \log_e \text{Stem}$$

$$r = 0.844, \text{adjusted } r^2 = 0.655, p < 0.001.$$

\log_e stem density increased with \log_e elevation, canopy cover, species richness and \log_e root weight (Table 3.59). The best predictor was canopy cover which explained 53.1% of variation in stem density. Prediction was not improved by combining these variables.

Table 3.60 Significant ($p \leq 0.05$) regression relationships between environmental, collective vegetation and dominant species trait variables measured at bank sub-sites in 2000.

Relationship	r	r ²	p
Species = $17.584 - 3.284 \log_e \text{ SP}$	-0.568	0.323	0.011
Species = $31.231 - 2.859 \log_e \text{ SN}$	-0.510	0.260	0.026
Species = $-7.726 + 2.718 \log_e \text{ Stem}$	+0.442	0.195	0.058
Species = $9.894 + 1.497 \log_e \text{ rwt}$	+0.565	0.319	0.023
Species = $25.769 - 18.563 \log_e \text{ Distance} + 4.334 \log_e \text{ Distance}^2$	0.638	0.332 (adj.)	0.015
$\log_e \text{ Biomass} = 5.363 + 0.016 \text{ Cover}$	+0.460	0.212	0.048
$\log_e \text{ Biomass} = 5.433 + 0.397 \log_e \text{ twt}$	+0.474	0.225	0.040
Height = $-5.659 + 9.056 \log_e \text{ SP} - 3.785 \log_e \text{ SP}^2 + 0.492 \log_e \text{ SP}^3$	0.456	0.346 (adj.)	0.025
Height = $0.375 + 0.275 \log_e \text{ twt}$	+0.634	0.402	0.002
Cover = $44.82 + 37.19 \log_e \text{ Elevation}$	+0.476	0.227	0.039
Cover = $-887.726 + 254.958 \log_e \text{ SN} - 16.898 \log_e \text{ SN}^2$	0.595	0.274	0.030
Cover = $-83.54 + 23.11 \log_e \text{ Stem}$	+0.729	0.531	<0.001
Cover = $-23.40 + 13.39 \log_e \text{ Biomass}$	+0.460	0.212	0.048
Cover = $44.99 + 17.72 \log_e \text{ lwt}$	+0.647	0.418	0.003
Cover = $68.277 + 8.616 \log_e \text{ rwt}$	+0.533	0.306	0.026
Cover = $29.371 + 14.112 \log_e \text{ twt}$	+0.581	0.337	0.009
$\log_e \text{ Stem} = 5.742 + 1.189 \log_e \text{ Elevation}$	+0.483	0.233	0.036
$\log_e \text{ stem} = 5.57989 + 0.0721197 \text{ Species}$	+0.447	0.200	0.055
$\log_e \text{ Stem} = 4.861 + 0.023 \text{ Cover}$	+0.729	0.531	<0.001
$\log_e \text{ Stem} = 6.527 + 0.301 \log_e \text{ rwt}$	+0.553	0.306	0.026

2001 B1 Bank

All of the environmental, vegetation and dominant species trait variables were normal either before or after square root or natural logarithm transformation. Significant Pearson product-moment correlation coefficients between pairs of variables are given in Table 3.61. Table 3.62 shows the regression equations which describe these relationships.

Correlation analysis showed that species richness decreased linearly with soil nitrogen and calcium (Table 3.61). Regression analysis showed that the amount of variation explained by soil nitrogen was greater if a quadratic relationship was considered (38.6%) but the simpler linear relationship between species richness and \log_e soil calcium explained more variation (42.4%).

Table 3.61 Significant ($p \leq 0.05$) Pearson product-moment correlation coefficients (r) between variables measured at B1 bank sub-sites in 2001.

Variable 1	Variable 2	r	p
Species	\log_e SN	-0.582	0.037
	\log_e Ca	-0.651	0.016
\log_e Biomass	\log_e Height	+0.802	0.001
	Cover	+0.818	0.001
	\log_e SLA	-0.647	0.023
Cover	\log_e SLA	-0.774	0.003
Stem	Distance	-0.606	0.028
\log_e slen	SP	-0.666	0.013
	\log_e SN	-0.740	0.004
	Fe	-0.574	0.040
\log_e rem	SpH	0.548	0.053

\log_e biomass increased linearly with \log_e canopy height and canopy cover, both of which explained a large and similar amount of variation, and decreased linearly with \log_e specific leaf area (Table 3.62). When \log_e canopy height and canopy cover were combined in a multiple regression, 82.2% of the variation in \log_e biomass was explained. These strong relationships indicate that it may be possible to make simple, quick, non-destructive measurements of canopy height and/or cover and to use these to make reliable predictions of vegetation biomass during monitoring of floodplain vegetation.

Cover decreased linearly with \log_e specific leaf area, increased linearly with \log_e biomass, and responded quadratically to \log_e calcium and stem density (Table 3.62). The strong relationship between \log_e biomass and canopy cover is described above. Specific leaf area was the next best predictor of canopy cover explaining 60% of the variation.

Stem density decreased linearly with distance from the water's edge. Distance explained 36.7% of the variation in stem density. This was the only significant predictor of stem density.

Three dominant species trait variables were related to environmental variables. \log_e stem length decreased linearly with \log_e soil nitrogen and iron. \log_e soil nitrogen was the more powerful predictor variable and explained 54.8% of the variation in \log_e stem length. \log_e leaf area and \log_e remainder weight both varied with soil pH, \log_e remainder weight increasing linearly and \log_e leaf area responding quadratically. Soil pH explained 41.3% of the variation in \log_e leaf area and 30% of the variation in \log_e remainder weight.

Table 3.62 Significant ($p \leq 0.05$) regression relationships between environmental, collective vegetation and dominant species trait variables measured at B1 bank sub-sites in 2001.

Relationship	r	r ²	p
Species = $105.786 - 23.8737 \log_e \text{SN} + 1.45453 \log_e \text{SN}^2$	0.699	0.386 (adj.)	0.035
Species = $29.973 - 2.536 \log_e \text{SN}$	-0.582	0.339	0.037
Species = $36.7330 - 3.61186 \log_e \text{Ca}$	-0.651	0.424	0.017
$\log_e \text{Biomass} = 6.529 + 1.003 \log_e \text{Height}$	+0.801	0.642	0.001
$\log_e \text{Biomass} = 3.300 + 0.038 \text{Cover}$	+0.818	0.670	0.001
$\log_e \text{Biomass} = 7.798 - 0.521 \log_e \text{SLA}$	-0.647	0.419	0.023
$\log_e \text{Height} = -4.758 + 0.641 \log_e \text{Biomass}$	+0.801	0.642	0.001
Cover = $-538.454033 + 173.194 \log_e \text{Ca} - 12.614 \log_e \text{Ca}^2$	0.676	0.348 (adj.)	0.047
Cover = $-43.792 + 17.506 \log_e \text{Biomass}$	+0.818	0.670	0.001
Cover = $-5.702 + 0.241 \text{Stem} - 0.000231 \text{Stem}^2$	0.683	0.466	0.043
Cover = $128.938 - 15.186 \log_e \text{SLA}$	-0.775	0.600	0.003
Stem = $676.441 - 87.9677 \text{Distance}$	-0.606	0.367	0.028
$\log_e \text{slen} = 6.44166 - 0.421307 \log_e \text{SN}$	-0.740	0.548	0.004
$\log_e \text{slen} = 3.96756 - 0.0152 \text{Fe (g)}$	-0.574	0.330	0.040
$\log_e \text{lar} = -23.3438 + 11.8051 \text{SpH} - 1.01866 \text{SpH}^2$	0.721	0.413	0.037
$\log_e \text{rem} = -5.144 + 0.866 \text{SpH}$	+0.548	0.300	0.053

2001 B2 Bank

Table 3.63 shows significant Pearson product-moment correlation coefficients calculated between pairs of normally distributed variables measured at B2 sub-sites. As stem density was not normally distributed, Spearman rank correlation coefficients were calculated for its relationships with other variables (Table 3.64). Regression equations describing significant relationships between pairs of normally distributed variables are given in Table 3.65.

Species richness at B2 sub-sites increased linearly with soil pH and decreased linearly with soil phosphorus, \log_e soil nitrogen and \log_e soil calcium (Table 3.63). The strongest relationship was with soil phosphorus which explained 36.6% of variation in species richness. Combining the predictors in multiple regression analysis did not increase the amount of variation explained.

Table 3.63 Significant ($p \leq 0.05$) Pearson product-moment correlation (r) coefficients between variables measured at B2 bank sub-sites in 2001.

Variable 1	Variable	r	p
Species	SpH	+0.484	0.036
	SP	-0.605	0.006
	log _e SN	-0.596	0.007
	log _e Ca	-0.550	0.015
log _e Biomass	Height	+0.530	0.024
Height	SLA	-0.477	0.045
	slen	+0.524	0.026
	rem	+0.609	0.006
	twl	+0.510	0.030
	Graze	-0.642	0.003
lwt	Graze	-0.551	0.018
lar	Graze	-0.497	0.036
slen	Graze	-0.558	0.016
rem	Graze	-0.586	0.008
twl	Graze	-0.622	0.006

Log_e biomass increased linearly with canopy height and responded cubically to soil iron (Table 3.65). Canopy height initially increased with iron then peaked and declined before again increasing at high iron.

Canopy height increased linearly with log_e biomass, stem length, remainder weight and total weight and decreased with specific leaf area and grazing score (Table 3.63).

Regression analysis showed that stem length and remainder weight were good predictors of canopy height, but the linear models describing the relationships with log_e biomass, total plant weight and specific leaf area did not fit the data well. Remainder weight was the best predictor of canopy height explaining 37.1% of the variation.

Spearman rank correlation coefficients showed that stem density tended to decrease with soil nitrogen, phosphorus and calcium and tended to increase with species richness and soil pH (Table 3.64).

Table 3.64 Significant ($p \leq 0.05$) Spearman rank correlation coefficients (r) between Stem (not normally distributed) and other variables measured at B2 bank sub-sites in 2001.

Variable 1	Variable 2	r	p
Stem	Ca	-0.571	0.011
	Species	+0.707	0.001
	SpH	+0.541	0.017
	SP	-0.443	0.057
	SN	-0.523	0.022

Table 3.65 Significant ($p \leq 0.05$) regression relationships between environmental, collective vegetation and dominant species trait variables measured at B2 bank sub-sites in 2001.

Relationship	r	r^2	p
Species = $-7.803 + 3.315 \text{ SpH}$	+0.484	0.234	0.036
Species = $15.099 - 0.255 \text{ SP}$	-0.605	0.366	0.006
Species = $26.342 - 2.085 \log_e \text{ SN}$	-0.596	0.356	0.007
Species = $27.112 - 2.395 \log_e \text{ Ca}$	-0.550	0.303	0.015
Species = $10.669 + 0.040 \text{ lar} - 0.000195 \text{ lar}^2 + 2 \times 10^{-7} \text{ Lar}^3$	0.672	0.335 (adj.)	0.033
$\log_e \text{ Biomass} = 3.197 + 0.260 \text{ Fe} - 0.006 \text{ Fe}^2 + 4.16 \times 10^{-5} \text{ Fe}^3 \text{ (g/kg)}$	0.720	0.415 (adj.)	0.014
$\log_e \text{ Biomass} = 5.212 + 0.926 \text{ Height}$	+0.530	0.281	0.024
Height = $-1.045 + 0.303 \log_e \text{ Biomass}$	+0.530	0.281	0.024
Height = $0.229 + 0.007 \text{ slen}$	+0.523	0.274	0.026
Height = $0.309 + 0.117 \text{ rem}$	+0.609	0.371	0.006

2000-2001 Bank

Significant Pearson correlation coefficients calculated between pairs of normally distributed variables measured over two years at bank sub-sites (2000 B and 2001 B2) are shown in Table 3.66. Equations describing the relationships between these variables are shown in Table 3.67.

Species richness was negatively correlated with \log_e soil phosphorus, \log_e soil nitrogen and \log_e soil calcium and positively correlated with shade and openness scores (Table 3.66). Regression analysis showed that \log_e soil phosphorus and \log_e soil nitrogen could each predict species richness in a linear relationship, soil phosphorus explaining slightly more variation than soil nitrogen. Residual analysis showed that \log_e calcium was not a suitable predictor. The two visually-assessed variables, shade and openness both varied significantly with species richness but the straight line produced for shade depended on a

very small number of sub-sites with scores above two. The line produced for openness had several sub-sites with each score and so the relationship was considered more reliable.

Table 3.66 Significant ($p \leq 0.05$) Pearson product-moment correlation coefficients (r) between variables measured at bank sub-sites in 2000 and 2001.

Variable 1	Variable 2	r	p
Species	\log_e SP	-0.576	<0.001
	\log_e SN	-0.534	0.001
	\log_e Ca	-0.359	0.027
	Shade	+0.436	0.006
	Open	+0.326	0.046
\log_e biomass	Height	+0.488	0.002
	Cover	+0.350	0.034
	slen	+0.514	0.001
	$\sqrt{\text{rem}}$	+0.498	0.002
	\log_e twt	+0.445	0.007
Height	\log_e lwt	+0.522	0.001
	\log_e lar	+0.364	0.027
	$\sqrt{\text{rem}}$	+0.560	<0.001
	\log_e twt	+0.637	<0.001
	slen	+0.648	<0.001
Cover	\log_e Graze	-0.523	0.001
	\log_e lwt	+0.363	0.027
	\log_e twt	+0.333	0.044
\log_e lwt	\log_e Graze	-0.502	0.002
\log_e lar	\log_e Graze	-0.537	0.001
$\sqrt{\text{rem}}$	\log_e Graze	-0.362	0.026
\log_e twt	\log_e Graze	-0.509	0.001

\log_e biomass increased linearly with canopy height, canopy cover, stem length, $\sqrt{\text{remainder weight}}$ and \log_e total plant weight (Table 3.66). Stem length was the best single predictor explaining 26.4% of the variation in \log_e biomass.

Canopy height increased linearly with five dominant species trait variables and with \log_e biomass (Table 3.66). Canopy height was also correlated with \log_e grazing score but this relationship depended on a very small number of sub-sites with grazing scores greater than two. Canopy height was best explained by the maximum stem length of the dominant species.

Canopy cover increased linearly with \log_e biomass, leaf weight and total plant weight, but the amount of variation explained by leaf weight was increased to 17.5% when a quadratic relationship was considered. The best single predictor was leaf area, which explained 23.5% of variation in canopy cover, also with a quadratic relationship.

The prediction of species richness, biomass, canopy height and canopy cover was not improved by combining the significant predictor variables in a multiple regression.

Table 3.67 Significant regression relationships between environmental, collective vegetation and dominant species trait variables measured at bank sub-sites in 2000 and 2001.

Relationship	r	r ²	p
Species = 26.963 - 2.231 \log_e SN	-0.534	0.285	0.001
Species = 19.468 - 3.675 \log_e SP	-0.575	0.331	<0.001
Species = 5.372 + 1.887 Open	+0.326	0.106	0.046
\log_e Biomass = 5.34 + 0.894 Height	+0.488	0.238	0.002
\log_e Biomass = 5.312 + 0.1226 Cover	+0.350	0.123	0.034
\log_e Biomass = 5.293 + 0.358 $\sqrt{\text{rem}}$	+0.498	0.248	0.002
\log_e Biomass = 5.376 + 0.383 \log_e twt	+0.445	0.198	0.007
\log_e Biomass = 5.252 + 0.829 slen	+0.514	0.264	0.001
Height = -0.812 + 0.272 \log_e Biomass	+0.488	0.271	0.001
Height = 0.667 + 0.257 \log_e lwt	+0.522	0.273	0.001
Height = -0.171 + 0.182 \log_e lar	+0.363	0.132	0.027
Height = 0.365 + 0.220 $\sqrt{\text{rem}}$	+0.560	0.314	<0.001
Height = 0.307 + 0.293 \log_e twt	+0.637	0.406	<0.001
Height = 0.277 + 0.570 slen	+0.648	0.420	<0.001
Cover = 3.917 + 10.105 \log_e Biomass	+0.350	0.123	0.034
Cover = 58.146 + 9.630 \log_e lwt	+0.361	0.132	0.027
Cover = 55.925 + 0.708 \log_e lwt + 6.466 \log_e lwt ²	0.470	0.175 (adj.)	0.014
Cover = 323.733 - 100.167 \log_e lar + 9.401 \log_e lar ²	0.527	0.235 (adj.)	0.004
Cover = 50.048 + 8.256 \log_e twt	+0.333	0.086	0.044

Stem density and specific leaf area were not normally distributed and so their relationships with other variables were tested by calculating Spearman rank correlation coefficients.

Significant results are shown in Table 3.68.

Stem density tended to decrease with soil nitrogen and increase with species richness.

Specific leaf area decreased with canopy height, canopy cover, remainder weight and total plant weight.

Table 3.68 Significant ($p \leq 0.05$) Spearman rank correlation coefficients (r) between Stem and SLA (not normally distributed) and other variables measured at bank sub-sites in 2000 and 2001.

Variable 1	Variable 2	r	p
Stem	SN	-0.367	0.023
	Spp	+0.563	<0.001
SLA	Height	-0.460	0.004
	Cover	-0.400	0.014
	rem	-0.376	0.022
	twl	-0.334	0.043

2000 C

Significant Pearson correlation coefficients calculated between pairs of normally distributed variables recorded at C sub-sites in 2000 are listed in Table 3.69. Predictive equations describing these relationships are shown in Table 3.70.

Biomass was positively correlated with canopy height and canopy cover and each of the dominant species trait variables, except for specific leaf area with which it was negatively correlated (Table 3.69). Regression analysis produced appropriate linear equations to describe the relationships of \log_e biomass with canopy cover, \log_e leaf weight, \log_e leaf area, specific leaf area, stem length, \log_e remainder weight and \log_e total plant weight. Residual analysis showed that a quadratic model fitted the relationship between \log_e canopy height and \log_e biomass better than a linear model (linear residuals were not normally distributed). \log_e canopy height was the best predictor, explaining 53.4% of the variation in \log_e biomass, while stem length was the best trait predictor. Combining stem length and canopy cover as predictor variables increased the amount of variation explained to 68.8% (Equation 3.4).

Equation 3.4

$$\log_e \text{ Biomass} = 3.58 + 0.966 \text{ slen} + 0.0180 \text{ Cover}$$

$$r = 0.850, \text{ adjusted } r^2 = 0.688, p < 0.001.$$

Table 3.69 Significant ($p \leq 0.05$) Pearson product-moment correlation (r) coefficients between variables measured at floodplain sub-sites in 2000.

Variable 1	Variable 2	r	p
Biomass	log _e Height	+0.612	0.005
	Cover	+0.580	<0.001
	lwt	+0.621	0.005
	SLA	-0.578	0.010
	lar	+0.490	0.033
	slen	+0.729	<0.001
	rem	+0.622	0.004
	twl	+0.675	0.002
log _e Height	lwt	+0.703	0.001
	lar	+0.616	0.005
	slen	+0.848	<0.001
	rem	+0.775	<0.001
	twl	+0.729	<0.001
	Graze	-0.492	0.033
Cover	Stem	+0.510	0.026
	Open	-0.709	0.001
	Shade	-0.618	0.005
log _e Stem	log _e Distance	+0.477	0.039
	Open	-0.496	0.031
	Shade	-0.546	0.016
log _e slen	log _e SP	+0.538	0.018
	SN	+0.512	0.025
	Graze	-0.468	0.043
SLA	Open	+0.504	0.028
	Shade	+0.479	0.038
log _e rem	Graze	-0.462	0.047

Log_e canopy height responded quadratically to specific leaf area and increased linearly with log_e leaf weight, log_e leaf area, stem length and log_e remainder weight (Table 3.70). Stem length was the best predictor, explaining 72% of the variation. Log_e canopy height was positively correlated with log_e biomass and log_e total plant weight and negatively correlated with log_e grazing score, but residual analysis showed that linear relationships with these variables did not fit the data well. The amount of variation explained increased only slightly if a quadratic relationship with stem length was considered, or if the predictor variables were combined in a multiple regression.

Canopy cover was positively correlated with \log_e stem density, but the linear regression did not fit the data well due to one outlier, EDB. The vegetation at this sub-site had been burnt recently and this could account for unusual percentage canopy cover and stem density measurements. Stem density was very high, but because the vegetation was mainly composed of seedlings, canopy cover was particularly low. If this sub-site is removed from the analysis, there is a strong, significant linear relationship between canopy cover and stem density. The linear relationship between canopy cover and \log_e biomass described previously explained a substantial amount of variation. Canopy cover also tended to decrease with openness and shade scores, but the straight lines describing these relationships depended on very few points.

Table 3.70 Significant ($p \leq 0.05$) regression relationships between environmental, collective vegetation and dominant species trait variables measured at floodplain sub-sites in 2000.

Relationship	r	r ²	p
$\log_e \text{ Biomass} = 6.352 + 1.462 \log_e \text{ Height} + 0.354 (\log_e \text{ Height})^2$	0.731	0.534 (adj.)	0.001
$\log_e \text{ Biomass} = 4.056 + 0.023 \text{ Cover}$	+0.580	0.336	0.009
$\log_e \text{ Biomass} = 5.743 + 0.308 \log_e \text{ lwt}$	+0.620	0.385	0.005
$\log_e \text{ Biomass} = 6.880 - 0.005 \text{ SLA}$	-0.578	0.334	0.010
$\log_e \text{ Biomass} = 4.314 + 0.272 \log_e \text{ lar}$	-0.490	0.240	0.033
$\log_e \text{ Biomass} = 4.725 + 1.108 \text{ slen}$	+0.729	0.531	<0.001
$\log_e \text{ Biomass} = 5.503 + 0.349 \log_e \text{ rem}$	+0.622	0.387	0.004
$\log_e \text{ Biomass} = 5.235 + 0.387 \log_e \text{ twt}$	+0.675	0.456	0.002
$\log_e \text{ Height} = -4.610 + 0.637 \log_e \text{ Biomass}$	+0.612	0.374	0.005
$\log_e \text{ Height} = -0.930 + 0.363 \log_e \text{ lwt}$	+0.704	0.495	0.001
$\log_e \text{ Height} = 1.309 - 0.018 \text{ SLA} + 2.73 \times 10^{-5} \text{ SLA}^2$	0.632	0.323 (adj.)	0.017
$\log_e \text{ Height} = -2.800 + 0.357 \log_e \text{ lar}$	+0.616	0.380	0.005
$\log_e \text{ Height} = -2.163 + 1.344 \text{ slen}$	+0.849	0.720	<0.001
$\log_e \text{ Height} = -1.237 + 0.453 \log_e \text{ rem}$	+0.775	0.601	<0.001
$\text{Cover} = -11.621 + 14.457 \log_e \text{ Biomass}$	+0.580	0.336	0.009
$\text{Cover} = -56.939 + 20.811 \log_e \text{ Stem (EDB deleted)}$	+0.750	0.562	<0.001
$\log_e \text{ Stem} = 4.289 + 0.027 \text{ Cover (EDB deleted)}$	+0.750	0.562	<0.001
$\log_e \text{ Stem} = 5.102 + 0.415 \log_e \text{ Distance}$	+0.476	0.227	0.039
$\log_e \text{ Stem} = 7.880 - 7.091 + 7.137 \text{ slen}^2 - 1.962 \text{ slen}^3$	0.684	0.361 (adj.)	0.021
$\log_e \text{ slen} = 0.231 + 0.000239 \text{ SN}$	+0.512	0.262	0.0249
$\log_e \text{ slen} = -0.380 + 0.504 \log_e \text{ SP}$	+0.538	0.289	0.018

\log_e stem density was positively correlated with \log_e distance and canopy cover, and negatively correlated with open and shade scores (Table 3.69). A linear relationship with \log_e distance explained 22.7% of the variation in \log_e stem density while a cubic

relationship with stem length explained 36.1%. Without EDB, a linear relationship with canopy cover explained 56.2% of the variation in \log_e stem density.

\log_e stem length increased linearly with \log_e soil phosphorus and soil nitrogen, \log_e soil phosphorus explaining slightly more variation (28.9%).

2001 C

Significant Pearson correlation coefficients calculated between pairs of variables measured at floodplain sub-sites in 2001 are listed in Table 3.71. Regression equations describing these relationships are shown in Table 3.72.

\log_e biomass increased linearly with canopy height, canopy cover, stem density, leaf weight, stem length and total plant weight and decreased as sub-sites became more enclosed by surrounding vegetation (Table 3.71). Regression analysis showed that quadratic relationships fitted the data better than linear relationships for the predictors canopy cover, stem density and stem length. \log_e biomass increased with these variables at low values, then reached a peak and declined slightly. Leaf weight was the best predictor of \log_e biomass (53.1% of variation explained) although the simpler measurement, canopy height, was also very good (49.3% of variation explained). Prediction was slightly improved by combining stem density with \log_e leaf weight (61.6% of variation explained) (Equation 3.5).

Equation 3.5

$$\log_e \text{ Biomass} = 4.25 + 0.008 \text{ Stem} - 9 \times 10^{-6} \text{ Stem}^2 + 0.641 \log_e \text{ lwt}$$

$$r = 0.822, \text{ adjusted } r^2 = 0.616, p < 0.001.$$

Species richness was predicted by just one variable, $\sqrt{\text{elevation}}$, which explained 35.1% of variation with a quadratic relationship (Table 3.72).

Canopy height was positively correlated with \log_e biomass, canopy cover, stem density, \log_e leaf weight, stem length, \log_e remainder weight and \log_e total plant weight and negatively correlated with openness and shade scores (Table 3.71). The best single predictor was \log_e leaf weight which explained 51.1% of the variation in canopy height.

Table 3.71 Significant ($p \leq 0.05$) Pearson product-moment correlation coefficients (r) between normally distributed variables measured at floodplain sub-sites in 2001.

Variable 1	Variable 2	r	p
log _e Biomass	Height	+0.702	0.001
	Cover	+0.493	0.027
	Stem	+0.545	0.013
	Open	-0.459	0.042
	lwt	+0.729	<0.001
	slen	+0.544	0.013
Height	twl	+0.460	0.048
	Cover	+0.453	0.045
	Stem	+0.488	0.029
	log _e lwt	+0.715	<0.001
	slen	+0.636	0.003
	log _e rem	+0.552	0.014
Cover	log _e twl	+0.611	0.005
	Open	-0.548	0.012
	Shade	-0.467	0.038
	Shade	-0.666	0.001
	Open	-0.683	0.001
	Stem	+0.520	0.019
Stem	slen	+0.499	0.025
	log _e twl	+0.471	0.042
	Open	-0.505	0.023
	Shade	-0.446	0.049
	log _e lwt	+0.521	0.019
	slen	+0.669	0.001
log _e lwt	log _e rem	+0.678	0.001
	log _e twl	+0.735	<0.001
	log _e Distance	-0.462	0.040
	Open	-0.638	0.002
log _e lar	Shade	-0.569	0.009
	log _e Distance	-0.508	0.022
	Open	-0.644	0.002
log _e rem	Shade	-0.619	0.004
	Open	-0.508	0.026
	Shade	-0.480	0.037
log _e twl	Open	-0.581	0.009
	Shade	-0.550	0.015

Canopy cover increased linearly with stem density, log_e biomass, stem length and log_e total plant weight, responded quadratically to canopy height and cubically to log_e leaf weight.

Canopy cover also declined with shade and as sites became more enclosed by surrounding vegetation. \log_e leaf weight was the best single predictor of canopy cover. At low leaf weight, cover initially decreased to a minimum. It then increased to a maximum at moderately high leaf weight before declining again at the greatest leaf weights.

Table 3.72 Significant regression relationships between environmental, collective vegetation and dominant species trait variables measured at floodplain sub-sites in 2001.

Relationship	r	r ²	p
Species = $17.434 - 21.084 \sqrt{\text{Elevation}} + 9.348 \text{ Elevation}$	0.647	0.351 (adj.)	0.010
$\log_e \text{ Biomass} = 4.938 + 1.353 \text{ Height}$	+0.702	0.493	0.001
$\log_e \text{ Biomass} = 3.982 + 0.075 \text{ Cover} - 0.0005 \text{ Cover}^2$	0.624	0.317 (adj.)	0.015
$\log_e \text{ Biomass} = 3.788 + 0.011 \text{ Stem} - 1.02 \times 10^{-5} \text{ Stem}^2$	0.672	0.387 (adj.)	0.006
$\log_e \text{ Biomass} = 5.686 + 0.834 \log_e \text{ lwt}$	+0.729	0.531	<0.001
$\log_e \text{ Biomass} = 2.460 + 0.070 \text{ slen} - 0.0003 \text{ slen}^2$	0.642	0.343 (adj.)	0.011
$\log_e \text{ Biomass} = 5.442 + 0.462 \log_e \text{ twt}$	+0.460	0.212	0.048
$\text{Height} = 0.436 + 0.007 \text{ Cover}$	+0.453	0.205	0.045
$\text{Height} = 0.346 + 0.001 \text{ Stem}$	+0.488	0.238	0.029
$\text{Height} = -1.369 + 0.365 \log_e \text{ Biomass}$	+0.702	0.493	0.001
$\text{Height} = 0.646 + 0.425 \log_e \text{ lwt}$	+0.715	0.511	<0.001
$\text{Height} = -0.014 + 0.009 \text{ slen}$	+0.636	0.405	0.003
$\text{Height} = 0.598 + 0.260 \log_e \text{ rem}$	+0.552	0.305	0.014
$\text{Height} = 0.306 + 0.353 \log_e \text{ twt}$	+0.611	0.373	0.005
$\text{Cover} = -3.354 + 135.774 \text{ Height} - 59.253 \text{ Height}^2$	0.563	0.237 (adj.)	0.039
$\text{Cover} = 23.382 + 0.091 \text{ Stem}$	+0.520	0.270	0.019
$\text{Cover} = -39.644 + 15.813 \log_e \text{ Biomass}$	+0.493	0.243	0.027
$\text{Cover} = 32.829 + 25.691 \log_e \text{ lwt} + 38.641 \log_e \text{ lwt}^2 - 21.048 \log_e \text{ lwt}^3$	0.675	0.353 (adj.)	0.019
$\text{Cover} = 14.778 + 0.449 \text{ slen}$	+0.499	0.249	0.025
$\text{Cover} = 30.861 + 16.874 \log_e \text{ twt}$	+0.471	0.222	0.042
$\text{Stem} = 1365.37 - 1560.19 \sqrt{\text{Elevation}} + 543.691 \text{ Elevation}$	0.597	0.281 (adj.)	0.024
$\text{Stem} = 218.353 + 171.469 \text{ Height}$	+0.488	0.238	0.029
$\text{Stem} = -36.549 + 14.249 \text{ Cover} - 0.101 \text{ Cover}^2$	0.653	0.358 (adj.)	0.009
$\text{Stem} = -241.166 + 99.434 \log_e \text{ Biomass}$	+0.545	0.297	0.013
$\text{Stem} = 311.629 + 108.765 \log_e \text{ lwt}$	+0.521	0.271	0.019
$\text{Stem} = 44.758 + 3.424 \text{ slen}$	+0.669	0.447	0.001
$\text{Stem} = 257.095 + 109.954 \log_e \text{ rem}$	+0.678	0.460	0.001
$\text{Stem} = 138.588 + 146.480 \log_e \text{ twt}$	+0.735	0.540	<0.001
$\log_e \text{ lwt} = 6.692 - 4.284 \log_e \text{ Distance} + 0.693 \log_e \text{ Distance}^2$	0.612	0.300 (adj.)	0.019
$\log_e \text{ lar} = 10.177 - 2.921 \log_e \text{ Distance} + 0.448 \log_e \text{ Distance}^2$	0.600	0.284 (adj.)	0.023

Stem density increased linearly with canopy height and biomass and with four of the dominant species trait variables (Table 3.71). It decreased with shade and as sub-sites

became more enclosed. Stem density was also quadratically related to $\sqrt{\text{elevation}}$ (gently decreasing to a minimum at lower values of $\sqrt{\text{elevation}}$ then rising again at higher values) and to canopy cover (rising gently at lower canopy cover then reaching a peak and reducing again at higher canopy cover). \log_e total plant weight was the best single predictor of stem density, explaining 54% of the variation. Stem density was slightly better predicted by combining the variables $\sqrt{\text{elevation}}$, elevation and \log_e biomass in a multiple regression (Equation 3.6).

Equation 3.6

$$\text{Stem} = 716\,541 \text{ elevation} - 1633 \sqrt{\text{elevation}} + 121 \log_e \text{ biomass}$$

$$r = 0.874, \text{ adjusted } r^2 = 0.720, p < 0.001.$$

Total leaf weight and total leaf area were both quadratically related to \log_e distance. Each variable generally decreased with \log_e distance, but increased slightly at the greatest distances.

2000-2001 C

Significant Pearson correlation coefficients are shown in Table 3.73, Spearman correlation coefficients in Table 3.74 and regression relationships in Table 3.75.

\log_e species richness was correlated with \log_e soil pH and \log_e soil nitrogen but residual analysis of the regression equations showed that only \log_e soil nitrogen was a suitable predictor. It explained 18.5% of the variation in \log_e species richness. Species richness also tended to increase with maximum stem length of the dominant species at each sub-site (Spearman rank correlation).

\log_e biomass was positively correlated with $\sqrt{\text{canopy height}}$, canopy cover, \log_e leaf weight (Pearson correlations), stem length, leaf area, remainder weight and total plant weight (Spearman correlations) and negatively correlated with \log_e specific leaf area and open and shade scores (Pearson correlations). Regression analysis showed that the relationships of \log_e biomass with canopy cover and leaf weight were better described by quadratic equations. It also showed additional quadratic relationships of \log_e biomass with stem density and soil phosphorus. The best single predictor was $\sqrt{\text{canopy height}}$, which explained 51.6% of the variation in \log_e biomass. \log_e leaf weight was the best dominant trait predictor, explaining 39.1%, and soil phosphorus the only environmental predictor,

explaining 11.9%. The amount of variation explained was maximised by combining the predictors $\sqrt{\text{canopy height}}$, $\log_e \text{stem density}$, $\log_e \text{stem density}^2$ and $\log_e \text{leaf weight}$ (Equation 3.7).

Equation 3.7

$$\log_e \text{Biomass} = -8.35 + 1.22 \sqrt{\text{Height}} + 4.04 \log_e \text{Stem} - 0.300 \log_e \text{Stem}^2 + 0.183 \log_e \text{lwt}$$

$$r = 0.833, \text{ adjusted } r^2 = 0.658, p < 0.001.$$

Square root canopy height increased linearly with \log_e biomass, \log_e soil phosphorus and \log_e leaf weight and decreased linearly with \log_e specific leaf area and openness score (Table 3.73). It also tended to increase with leaf area, remainder weight, stem length and total weight (Table 3.74). Regression analysis also revealed quadratic relationships with canopy cover and stem density. The previously described relationship between $\sqrt{\text{canopy height}}$ and \log_e biomass explained the greatest amount of variation in canopy height. \log_e leaf weight was the next best single predictor, explaining 48.9% of the variation. The amount of variation explained was increased slightly by combining the predictors \log_e soil phosphorus and \log_e leaf weight in a multiple regression (Equation 3.8).

Equation 3.8

$$\sqrt{\text{Height}} = 0.473 + 0.105 \log_e \text{SP} + 0.123 \log_e \text{lwt}$$

$$r = 0.736, \text{ adjusted } r^2 = 0.541, p < 0.001.$$

Canopy cover increased linearly with \log_e stem density and \log_e biomass and decreased as sites became more shaded and enclosed by surrounding vegetation (Table 3.73). A quadratic relationship with \log_e stem density explained the greatest amount of variation in canopy cover (35.4%). Canopy cover generally increased with \log_e stem density but more rapidly at low stem density and more slowly at high stem density.

\log_e stem density increased linearly with \log_e distance and canopy cover and decreased linearly with \log_e soil phosphorus and open and shade scores (Table 3.73). \log_e stem density responded quadratically to \log_e soil pH, \log_e calcium, $\sqrt{\text{canopy height}}$ and \log_e leaf weight. \log_e stem density increased steeply with \log_e soil pH at low pH, then reached a maximum and slightly declined at higher pH. \log_e stem density was relatively unaffected by \log_e calcium at low levels, but began to decrease at higher levels of \log_e calcium.

Table 3.73 Significant ($p \leq 0.05$) Pearson product-moment correlation coefficients (r) between normally distributed variables measured at 2000-2001 floodplain sub-sites.

Variable 1	Variable 2	R	p
\log_e Species	\log_e SpH	+0.365	0.022
	\log_e SN	-0.431	0.007
\log_e Biomass	$\sqrt{\text{Height}}$	+0.718	<0.001
	Cover	+0.460	0.003
	\log_e lwt	+0.621	<0.001
	\log_e SLA	-0.561	<0.001
	Open	-0.411	0.009
	Shade	-0.345	0.031
	\log_e SP	+0.402	0.012
$\sqrt{\text{Height}}$	\log_e lwt	+0.699	<0.001
	\log_e SLA	-0.533	<0.001
	Open	-0.318	0.049
	\log_e Stem	+0.561	<0.001
Cover	Open	-0.684	<0.001
	Shade	-0.637	<0.001
	\log_e Distance	+0.353	0.027
\log_e Stem	\log_e SP	-0.333	0.041
	Open	-0.449	0.004
	Shade	-0.472	0.002
	\log_e Distance	-0.344	0.032

Canopy cover was the best single predictor of \log_e stem density (31.4% of variation explained). The amount of variation explained was increased by combining some of these predictors (Equation 3.9).

Equation 3.9

$$\log_e \text{ Stem} = 4.27 + 0.229 \log_e \text{ Distance} + 0.0145 \text{ Cover} + 0.0822 \log_e \text{ lwt}^2$$

$$r = 0.791, \text{ adjusted } r^2 = 0.593, p < 0.001.$$

Finally, \log_e leaf weight decreased linearly with \log_e distance which explained 11.9% of the variation.

Table 3.74 Significant ($p \leq 0.05$) Spearman rank correlation coefficients (r) between lar, slen, rem and twt (not normally distributed) and other variables measured at 2000-2001 C sub-sites.

Variable 1	Variable 2	r	p
Species	slen	+0.479	0.022
Biomass	slen	+0.477	0.002
	lar	+0.522	0.001
	rem	+0.541	0.000
	twt	+0.622	0.000
	Height		
Height	lar	+0.557	0.000
	slen	+0.644	0.000
	rem	+0.740	0.000
	twt	+0.750	0.000
Slen	Distance	-0.347	0.030
Slen	Elevation	-0.400	0.012
Slen	SP	-0.317	0.052

Table 3.75 Significant regression relationships between environmental, collective vegetation and dominant species trait variables at 2000-2001 floodplain sub-sites.

Relationship	r	r ²	p
$\log_e \text{ Spp} = 3.965 - 0.253 \log_e \text{ SN}$	-0.430	0.185	0.007
$\log_e \text{ biomass} = 1.202 + 3.198 \log_e \text{ SP} - 0.510 \log_e \text{ SP}^2$	0.409	0.119 (adj.)	0.041
$\log_e \text{ biomass} = 4.109 + 2.246 \sqrt{\text{Height}}$	+0.718	0.516	<0.001
$\log_e \text{ biomass} = 3.596 + 0.076 \text{ Cover} - 0.0005 \text{ Cover}^2$	0.583	0.303 (adj.)	0.001
$\log_e \text{ biomass} = -19.617 + 8.224 \log_e \text{ Stem} - 0.651 \log_e \text{ Stem}^2$	0.619	0.348 (adj.)	<0.001
$\log_e \text{ biomass} = 5.694 + 0.425 \log_e \text{ lwt} + 0.047 \log_e \text{ lwt}^2$	0.650	0.391 (adj.)	<0.001
$\log_e \text{ biomass} = 10.424 - 0.860 \log_e \text{ SLA}$	-0.561	0.315	<0.001
$\sqrt{\text{Height}} = -0.557 + 0.230 \log_e \text{ Biomass}$	+0.718	0.516	<0.001
$\sqrt{\text{Height}} = 0.302 + 0.172 \log_e \text{ SP}$	+0.401	0.161	0.012
$\sqrt{\text{Height}} = 0.286 + 0.018 \text{ Cover} + 1.289 \times 10^{-4} \text{ Cover}^2$	0.390	0.105 (adj.)	0.052
$\sqrt{\text{Height}} = -5.933 + 2.276 \log_e \text{ Stem} - 0.189 \log_e \text{ Stem}^2$	0.509	0.218 (adj.)	0.004
$\sqrt{\text{Height}} = 0.773 + 0.137 \log_e \text{ lwt}$	+0.699	0.489	<0.001
$\sqrt{\text{Height}} = 2.172 - 0.261 \log_e \text{ SLA}$	-0.533	0.284	<0.001
$\text{Cover} = -383.428 + 129.368 \log_e \text{ Stem} - 9.012 \log_e \text{ Stem}^2$	0.623	0.354 (adj.)	<0.001
$\text{Cover} = -13.793 + 13.108 \log_e \text{ Biomass}$	+0.459	0.211	0.003
$\log_e \text{ Stem} = 5.131 + 0.330 \log_e \text{ Distance}$	+0.354	0.125	0.027
$\log_e \text{ Stem} = -19.805 + 30.488 \log_e \text{ SpH} - 8.867 \log_e \text{ SpH}^2$	0.392	0.107 (adj.)	0.049
$\log_e \text{ Stem} = 7.047 - 0.357 \log_e \text{ SP}$	-0.333	0.111	0.041
$\log_e \text{ Stem} = -7.297 + 4.002 \log_e \text{ Ca} - 0.297 \log_e \text{ Ca}^2$	0.395	0.107 (adj.)	0.052
$\log_e \text{ Stem} = 7.748 - 4.876 \sqrt{\text{Height}} + 2.962 \text{ Height}$	0.385	0.101 (adj.)	0.055
$\log_e \text{ Stem} = 5.052 + 0.016 \text{ Cover}$	+0.560	0.314	<0.001
$\log_e \text{ Stem} = 5.757 + 0.039 \log_e \text{ lwt} + 0.104 \log_e \text{ lwt}^2$	0.550	0.264 (adj.)	0.002
$\log_e \text{ lwt} = 2.025 - 0.662 \log_e \text{ distance}$	-0.345	0.119	0.032

3.4.5 Testing the outcomes of the analyses

Testing 2000-2001 TWINSpan results with the 2002 data set: Bank sub-sites

Although less species information was available in 2000 and 2001 than in 2002, it was still possible to assign the sub-sites sampled in 2002 to the TWINSpan groups produced by analysis of the 2000-2001 data set according to their species assemblages. The species recorded at CAR2, TIA, FRA and JAC corresponded with those characteristic of 2000-2001 TWINSpan group Ia while those at LP3 and CID suggested that these sub-sites were associated with group Ib. The species assemblages at MAN and PDG suggested that they belonged to group I rather than group II, but they did not match either sub-group closely.

ZEM, BFP3, IVI2 and RPM3 supported species associated with group IIa while CUR4 was the only sub-site with a similar species assemblage to group IIb.

Table 3.76 Mean and standard error of environmental, collective vegetation and dominant species trait variables in 2000-2001 TWINSpan group I and 2002 sites assigned to TWINSpan group I. The p-value indicates the significance of difference between the means determined by a t-test.

Variable	2000-2001	S.e.	2002	S.e.	p
	Group I		Group I		
Sediment total ext. P mgkg ⁻¹	25.09	1.88	20.40	6.26	0.274
Sediment TKN mgkg ⁻¹	8116	2421	3610	1059	0.217
Soil total Ca (mgkg ⁻¹)	3043	816	1336	196	0.198
Canopy cover %	76.34	3.97	85.90	5.97	0.207

Table 3.77 Mean and standard error of environmental, collective vegetation and dominant species trait variables in 2000-2001 TWINSpan group II and 2002 sites assigned to TWINSpan group II. The p-value indicates the significance of difference between the means determined by a t-test.

Variable	2000-2001	S.e.	2002	S.e.	p
	Group I		Group I		
Sediment total ext. P mgkg ⁻¹	15.40	2.60	13.00	4.16	0.835
Sediment TKN mgkg ⁻¹	3110	775	3126	808	0.541
Soil total Ca (mgkg ⁻¹)	1175	199	702	189	0.202
Canopy cover %	61.48	5.26	85.44	9.67	0.072

When vegetation and environment characteristics which distinguished TWINSpan groups I and II in the 2000-2001 data set were compared between these groups and 2002 sites assigned to these groups, no significant differences were found (Table 3.76 and Table 3.77). Sediment phosphorus, nitrogen and calcium and vegetation percentage canopy cover were similar between 2000-2001 group I sites and 2002 sites assigned to that group and between 2000-2001 group II sites and 2002 sites assigned to that group.

Testing 2000-2001 TWINSpan results with the 2002 data set: Floodplain sub-sites

The species assemblages of the C sub-sites sampled in 2002 did not closely correspond to those of the 2000-2001 TWINSpan groups. At two of the sites, the shrub *Galeanthe brasiliensis* was the dominant species whereas in 2000 and 2001 it tended not to be dominant but was present in mixed communities at relatively low abundance. Although

Poaceae was also abundant at these sites, it was difficult to assign them to TWINSpan groups. Some sub-sites appeared to fit equally well into TWINSpan groups IV and V, perhaps suggesting that divisions should have been stopped at an earlier stage in the TWINSpan analysis. Most sub-sites were more closely associated with groups IV and V than with the other groups. Due to the difficulty of assigning the 2002 sub-sites to the 2000-2001 TWINSpan groups, vegetation and environmental variables were not compared between the two data sets.

Testing the regression equations derived from the 2000-2001 data set

B sub-sites

The prediction of species richness by soil nitrogen and phosphorus were the only vegetation-environment relationships detected for bank sub-sites in the 2000-2001 data set. When these relationships were tested using the 2002 data, the predicted species richness did not correspond with the measured species richness (Table 3.78). Biomass, canopy height and canopy cover measurements made in 2002 were each well predicted from collective vegetation and dominant species trait variables using the regression equations (Table 3.78).

Table 3.78 Pearson product-moment correlation coefficients (*r*) calculated between variables measured at *B* sub-sites in 2002 and the values of these variables predicted using regression relationships derived from 2000-2001 data.

Significant 2000-2001 relationship	<i>r</i> (2002 actual v predicted)	<i>p</i>
Species = $19.468 - 3.675 \log_e SP$	-0.149	0.627
Species = $26.963 - 2.231 \log_e SN$	-0.138	0.654
\log_e Biomass = $5.252 + 0.829 \text{ slen}$	+0.643	0.018
Height = $0.277 + 0.570 \text{ slen}$	+0.553	0.050
Cover = $92.4 - 16.6 \log_e \text{lar} + 49.9 \sqrt{\text{rem}} - 9.80 \text{rem} + 11.1 (\log_e \text{lw})^2$	-0.604	0.029
Cover = $323.733 - 100.167 \log_e \text{lar} + 9.401 (\log_e \text{lar})^2$	-0.906	<0.001
Cover = $38.431 + 13.202 \log_e \text{tw}$	+0.625	0.022

C sub-sites

Table 3.79 Pearson product-moment correlation coefficients (*Spearman rank correlation coefficient for non-normal data) (r) calculated between variables measured at C sub-sites in 2002 and the values of these variables predicted using regression relationships derived from 2000-2001 data.

2000-2001 relationship	r (2002 actual v predicted)	p
$\log_e \text{ Species} = 3.965 - 0.253 \log_e \text{ SN}$	-0.064	0.836
$\log_e \text{ biomass} = -8.35 + 1.22 \sqrt{\text{ht}} + 4.04 \log_e \text{ stem} - 0.30 (\log_e \text{ stem})^2 + 0.183 \log_e \text{ lwt}$	0.749	0.003
$\log_e \text{ biomass} = 4.109 + 2.246 \sqrt{\text{Height}}$	+0.893	<0.001
$\log_e \text{ biomass} = 1.202 + 3.198 \log_e \text{ SP} - 0.510 (\log_e \text{ SP})^2$	0.571	0.042
$\sqrt{\text{Height}} = 0.473 + 0.105 \log_e \text{ SP} + 0.123 \log_e \text{ lwt}$	0.890	<0.001
$\sqrt{\text{Height}} = 0.773 + 0.137 \log_e \text{ lwt}$	+0.748	0.003
$\sqrt{\text{Height}} = 0.302 + 0.172 \log_e \text{ SP}$	+0.739	0.004
$\log_e \text{ Stem} = 4.27 + 0.229 \log_e \text{ distance} + 0.0145 \text{ Cover} + 0.0822 (\log_e \text{ lwt})^2$	0.700	0.008
$\log_e \text{ Stem} = 5.052 + 0.016 \text{ Cover}$	+0.613	0.026
$\log_e \text{ Stem} = -7.297 + 4.002 \log_e \text{ Ca} - 0.297 (\log_e \text{ Ca})^2$	*-0.596	0.032
$\log_e \text{ lwt} = 2.025 - 0.662 \log_e \text{ distance}$	-0.082	0.790

At C sub-sites, the responses predicted from the regression equations were, in most cases, significantly and highly correlated with the measured responses (Table 3.79). This result indicates that the predictive equations were realistic, describing genuine vegetation patterns in the floodplain. Some of the relationships are unsurprising, such as the relationship between the height of the vegetation canopy and its biomass. However, it is particularly useful to know that this relationship is robust as it indicates that non-destructive canopy height measurements could replace destructive and time-consuming biomass sampling as a way of monitoring vegetation without losing much information. The relationships of biomass and height with soil phosphorus content and stem density with soil calcium content describe vegetation responses to the soil chemical environment and therefore allow the effect of a change in this factor to be predicted.

3.5 Discussion

3.5.1 Vegetation Communities

Comparison of analyses of bank species data

Bank sub-sites included gently sloping lagoon shores where there was a gradual transition from open water to a grass or *Polygonum*-dominated wetland, banks of backwaters where tree canopies extended over the water, and near-vertical eroded banks where terrestrial vegetation suddenly met a river channel. During TWINSpan analysis, the major contrasts between bank types were indicated by a small number of relatively abundant plant groups. The most significant of these were the *Polygonum* species ("*Polygonum* sp." and each of the individual species which were identified), *Ludwigia* sp., *Commelina* sp., Poaceae, Cyperaceae and creepers. In each of the data sets investigated, the sites at which *Polygonum* species were abundant were separated from the other sites from which they tended to be absent. In 2000, the main division in the species data was between a group of sites supporting *Polygonum* sp., *Ludwigia* sp., *Commelina* sp. and *Mimosa* sp. and a group of sites from which these species were absent. In the 2001 B2 species data, sites supporting *Polygonum* sp. and *Ludwigia* sp. were separated from sites which did not support these species but in which grasses and creepers were important. The pattern was broken in the 2001 B1 data set when the two groups consisted of one in which *Polygonum* sp. and Cyperaceae were important and one which supported *Ludwigia* sp., *Commelina* sp., *Eleocharis* sp. and creepers. If the two previously identified vegetation groupings were related to water availability at the sub-sites as suggested above, then the division of these two hybrid groups could be due to the absence of dry sites in this data set, as B1 sites were the temporarily exposed beds of waterbodies. These two groups may be sub-groups of the *Polygonum*-*Ludwigia* community. When the B1 and B2 sub-sites were analysed together, these two sub-groups were again observed. However, a group in which *Polygonum* sp. and *Ludwigia* sp. were absent was also produced. Poaceae, creepers, woody plants and ferns were characteristic of this group. Combined analysis of 2000 B and 2001 B2 sub-sites produced two main groups and four sub-groups. The two broad groupings consisted of one in which *Polygonum* species and *Ludwigia* sp. were important and another in which these were rare but Poaceae, ferns, creepers and woody plants were important. The *Polygonum*-*Ludwigia* group tended to be associated with high soil phosphorus, nitrogen and calcium and low elevation. These sub-sites were usually adjacent to open lagoons and were gently sloping, unshaded and open. The Poaceae group generally occurred at sub-sites with lower

soil phosphorus, nitrogen and calcium and higher elevation. These banks were steeper, less open, more shaded and often adjacent to flowing channels. Vegetation characteristics were variable between the two groups although the *Polygonum-Ludwigia* group tended to have higher canopy cover than the Poaceae group. The sub-groups of the *Polygonum* group consisted of one in which *Polygonum* species occurred with *Commelina* sp. and Poaceae and a second in which *Polygonum* species occurred with creepers. The sub-groups of the Poaceae group consisted of one in which Poaceae occurred with ferns and *Mimosa* sp. and one in which Poaceae was highly dominant.

By examining the species assemblage at each sub-site sampled in 2002, these sub-sites were assigned to the most appropriate TWINSpan vegetation type identified from the 2000-2001 data set. The vegetation and environmental characteristics which had previously been found to distinguish these groups did not differ significantly between the 2000-2001 sub-sites comprising the TWINSpan groups and the 2002 sub-sites assigned to these groups.

Comparison of analyses of floodplain species data

In 2000, two main groups of sites were produced. The first was characterised by creepers, Cyperaceae and *Mimosa* sp. and the second by *Ludwigia* sp., *Polygonum* sp. and woody plants. Poaceae was common across both groups. In the 2001 data set, there was also a division influenced by the distribution of creepers. The first major division produced a group in which creepers occurred together with Poaceae and woody plants and a group in which creepers and Poaceae tended not to occur. *Polygonum* sp. and *Polygonum stelligerum* were characteristic of this second group. The creeper-Poaceae vegetation type tended to occur at sub-sites associated with flowing channels and backwaters where soil phosphorus, nitrogen, calcium and iron were low and soil pH was less acidic. These sites were sometimes less open and more shaded than those associated with the *Polygonum* group. The *Polygonum* group was associated with open, unshaded, ungrazed sub-sites adjacent to open lagoons where the soil was acidic and high in phosphorus, nitrogen, calcium and iron.

When the two data sets were combined, several small groups were produced during TWINSpan analysis. The first division made a group of the sites which had formed the *Polygonum*-indicated group in 2000, together with one further site sampled in 2001. The remaining sites were associated with Poaceae and creepers. This large Poaceae-creeper group was then divided to produce a group in which creepers were abundant but Poaceae

was rare and a larger group in which Poaceae was abundant but creepers were not. Finally, this Poaceae group was divided into two groups of sub-sites which were both dominated by Poaceae but one tended also to support creepers while the other did not.

The groupings suggested that there could be a number of different communities in which Poaceae played a part, for example 2000-2001 groups IV and V. In group IV, grasses co-occurred with creepers but in group V creepers tended not to occur. Group III sites also tended to be dominated by Poaceae with few creepers, but *Ludwigia* sp. was also important in this group. On the other hand, some sites were dominated by creepers with just a low frequency of grasses (2000-2001 group II), while neither creepers nor grasses were important in group I which was characterised by *Polygonum* sp.. Identification of the creepers and grasses to species level could help to reveal these vegetation sub-types.

The species assemblages recorded at C sub-sites in 2002 did not correspond closely with those recorded in 2000 and 2001. The 2002 sub-sites therefore did not fit easily into the vegetation types represented by the 2000-2001 TWINSpan groups. TWINSpan analysis of the 2000-2001 data set may not have identified the major vegetation groups of floodplain areas but focused on sub-groups which were not observed in 2002. This could suggest that the number of C sub-sites sampled was too few to represent the vegetation groups occurring across the floodplain. As plant diversity was so high, with very few sub-sites sharing the same species, rare species may have influenced the formation of the TWINSpan groups, obscuring larger scale patterns in the vegetation of the C sub-sites. Low floristic similarity between neighbouring forest formations in the study area have been reported, with a high proportion of species occurring exclusively at single sites (Agostinho, Thomaz & Hahn 2004).

3.5.2 Predictive relationships

Bank

During the analyses of the data collected in 2000 and 2001, several environmental predictors of species richness were found. These were soil phosphorus, soil nitrogen, soil calcium, soil pH, site openness and the distance of the sub-site from the associated waterbody. Species richness tended to be lower at more sheltered sites with more fertile soils. These favourable conditions for growth may have stimulated competitive interactions between species, resulting in the dominance of a small number of the most competitive species. Biomass responded cubically to soil iron and canopy height to soil

phosphorus, suggesting complex relationships of soil nutrients (and potentially toxic iron, when at high levels) with production. Canopy cover responded quadratically to soil nitrogen and soil calcium and increased with the elevation of the sub-site above the associated waterbody. Stem density increased with the elevation above the associated waterbody and decreased with distance from it, which could reflect variations in soil moisture. Stem length decreased with soil nitrogen and soil iron. Leaf area responded quadratically to soil pH and remainder weight increased with soil pH. Variation in these environmental variables is therefore associated with variation in the vegetation of the banks and shores of the floodplain waterbodies. Future changes in these variables could be expected to cause a response in the vegetation.

There were also several relationships between collective vegetation and dominant species trait variables. Increasing species richness was associated with increasing stem density, possibly because higher stem density indicated a greater number of plants and therefore a greater likelihood of more species occurring. As could be expected, biomass increased with the size of the dominant species, canopy height and canopy cover, indicating that future studies of this vegetation could use simple non-destructive sampling methods to predict biomass. Stem density increased with canopy cover and root weight of the dominant species.

Vegetation variables tended to be best predicted by dominant species trait variables or by other vegetation variables. These relationships were successfully used to predict vegetation variables in the 2002 test data set. In the two-year data set, few vegetation-environment relationships were observed. Species richness was significantly predicted by soil nitrogen and phosphorus but this relationship did not predict species richness successfully in the 2002 data set.

Floodplain

Environmental predictors of species richness found during analysis of the two years of data were elevation of the sub-site above the associated waterbody (quadratic), possibly reflecting an effect of water availability, and soil nitrogen (a negative linear relationship), suggesting that low nutrient availability limited species richness at some sub-sites.

Biomass and canopy cover were predicted only by collective vegetation and dominant species trait variables. Canopy height increased with soil phosphorus. Stem density responded quadratically to elevation above the associated waterbody and to soil pH and calcium, increased with distance from the waterbody and decreased with soil phosphorus.

Higher levels of soil phosphorus therefore stimulated the development of taller, less dense communities. Stem length increased with soil nitrogen and phosphorus, leaf weight decreased with distance from the waterbody while leaf area responded quadratically.

Species richness was not related to any other collective vegetation or dominant species trait variable, but there were several other relationships within these two groups of variables. Biomass tended to increase with each of the collective vegetation and dominant species trait variables (except for specific leaf area with which it decreased), although some levelling off was seen at the greatest measurements of canopy height, canopy cover, stem density, stem length and leaf weight. Canopy height also tended to increase with canopy cover, stem density and biomass but decreased slightly at the greatest canopy heights. Canopy height increased with the dominant species trait variables, except for specific leaf area with which it decreased. Canopy cover tended to increase with stem density, canopy height, biomass, stem length and total plant weight but again sometimes showed some decrease at the greatest heights and stem densities. Stem density tended to increase with canopy cover, canopy height and biomass but showed some decrease at the greatest canopy heights and covers. Stem density also increased with stem length, remainder weight, leaf weight and total plant weight.

Very few statistically significant vegetation-environment relationships were observed in the 2000-2001 data set. The relationship of species richness with soil nitrogen did not successfully predict species richness in the 2002 test data set. However, the prediction of biomass was much more successful. Three equations, one with soil phosphorus as a single predictor, another with canopy height as a single predictor and a third with canopy height, stem density and leaf weight as predictors, explained biomass well in the 2000-2001 data set and also in the 2002 data set. Soil phosphorus and leaf weight were both good predictors of canopy height and explained even more variation when combined in a multiple regression. This equation also successfully predicted canopy height in the 2002 data set. The equations derived from the 2000-2001 data set relating stem density to environmental and vegetation variables each successfully predicted this variable in the 2002 data set. When applied to the 2002 data set, distance did not successfully predict leaf area.

3.6 Conclusions

- TWINSpan analysis of Bank data suggested two major vegetation types; a *Polygonum-Ludwigia* community and a Poaceae community in which ferns, creepers and woody plants were also important.
- The *Polygonum-Ludwigia* group was associated with low elevation banks which sloped gently from open lagoons. Soils tended to be high in nitrogen, phosphorus and calcium.
- The Poaceae group was associated with high elevation, steep banks adjacent to flowing channels. Soils were lower in nitrogen, phosphorus and calcium.
- A *Polygonum-Commelina* community and a *Polygonum*-creeper community were suggested as sub-groups of the *Polygonum* vegetation type.
- The Poaceae group could also be broken down into sub-groups, one in which Poaceae was highly dominant and a second mixed Poaceae-*Mimosa*-fern community.
- The floodplain species data also indicated two contrasting vegetation types, one characterised by *Polygonum* and a second in which creepers and Poaceae were important.
- Most of the sites sampled supported vegetation of the Poaceae-creeper type, and analysis of the two-year data set suggested that there were several different sub-communities in which creepers and Poaceae played varying roles.
- Regression relationships derived from the 2000-2001 C data set successfully predicted canopy height, biomass and stem density in the 2002 data set from both environmental and vegetation variables.
- The regression equations derived from the B data set were less generally applicable but canopy height, biomass and cover were successfully predicted by dominant species trait variables in the 2002 data set.

- In both B and C data sets, canopy height, percentage canopy cover, stem density and biomass all tended to be inter-correlated although the response variable sometimes reached a maximum or decreased at the highest values of the predictor variable.
- In both B and C 2000-2001 data sets, few vegetation-environment relationships were found. However, analysis of the individual years suggested potential relationships between sub-site physical and chemical characteristics and the vegetation growing there.
- Analysis of C sub-site data (individual years) showed relationships between species richness and soil nitrogen, biomass and soil phosphorus, canopy height and soil phosphorus, stem density and elevation, distance, soil pH, soil phosphorus and soil calcium, stem length and soil nitrogen and soil phosphorus, leaf weight and distance and leaf area and distance.
- Analysis of B sub-sites data (individual years) showed relationships between species richness and soil phosphorus, nitrogen, calcium, pH and distance from the associated waterbody; biomass and soil iron; canopy height and soil phosphorus; canopy cover and soil calcium and elevation; stem density and elevation and distance from the waterbody; stem length and soil nitrogen, phosphorus and iron; total leaf area and soil pH; and remainder weight and soil pH.
- These relationships provide a tool for suggesting possible consequences for the vegetation of future changes in these environmental variables.

4 Impacts of cattle grazing on island and floodplain vegetation

4.1 Aims

- To investigate the impact of short-term biomass removal from an area of apparently natural vegetation that showed no signs of being grazed by either livestock or native herbivores.
- To quantify the impact of cattle grazing upon herbaceous vegetation on a small farm on Mutum Island.
- To evaluate the potential for recovery of this vegetation following protection from grazing pressure.
- To investigate the effect of an increase in soil nutrients on grazed and ungrazed vegetation on Mutum Island.

4.2 Introduction

Grazing by cattle is the most noticeable anthropogenic impact acting on the vegetation of the drier areas of the floodplain, including the islands in the Paraná channel. Although the keeping of cattle on the islands included in the Environmental Protection Area has officially been banned, some small scale farmers still graze their animals on parts of the islands. The effect on the vegetation tends to be severe, resulting in very low sward heights and bare ground. Crops are also grown on some farms but this was observed only on a small scale.

During the field surveys, grazing intensity was recorded at each sub-site by visual assessment of the amount of damage to the vegetation that appeared to have been caused by grazing. The observations indicated that grazing intensity varied across the study sites and was very high in some areas. It was therefore decided to further investigate grazing impacts by means of manipulative field experiments. Two different approaches were employed to compare grazed vegetation with ungrazed vegetation and thus quantify the impact of grazing disturbance. These involved i) creating an artificial disturbance by cutting vegetation in plots of apparently natural wet grassland and ii) protecting plots of

heavily grazed island vegetation using grazing exclosures. In the second design, an additional factor, nutrient supply, was introduced into the experiment. The reduction in the frequency and intensity of flood events in the Paraná River caused by upstream dams is likely to lead to reduced vegetation decomposition and nutrient cycling processes in the floodplain (Thomaz, Roberto & Bini 1997). This in turn would probably reduce the supply of plant nutrients to the soil of the seasonally inundated areas. Due to the practical difficulties of reducing soil nutrients in the experiment, it was decided to apply fertiliser to half of the plots and so investigate whether the current vegetation type was nutrient-limited or if the addition of nutrients would stimulate further growth.

4.3 Methods

4.3.1 Experiment 1: Impacts of disturbance (comparable to a single severe grazing event) on the structure of natural floodplain vegetation

An isolated area of wetland in the floodplain of the Baía River was chosen as the site for this study because it appeared to be free from human or grazing disturbance, with the vegetation height generally in the range 1.2–2.2m high (Figure 4.1).



Figure 4.1 The site of the cutting experiment, an area of tall wet grassland adjacent to the Baía River.

The area was close to Lagoa Traíra (LATR, surveyed in 2001) where the floodplain is flat and low-lying, with the water table close to the surface. The vegetation was dominated by tall, wetland grasses such as *Panicum pernambucense* and *Paspalum conspersum*. On 24

September 2001, nine plots of 1m x 1m were selected (GPS location plot 1 S 22°44.574' W 53°20.527; plot 9 S 22°44.591' W 53°20.487') and cutting treatments randomly assigned in three blocks. Within each block, one plot was left uncut, one was cut down to leave a sward height of 50cm, and the remaining plot was cut down to ground level, leaving no vegetation canopy within the square metre area. All cut vegetation was removed from the plots. Figure 4.2 shows a plot immediately after the vegetation has been partially cut to leave a sward height of 50cm.



Figure 4.2 Cutting experiment: A 1m² plot in which vegetation has been cut down to leave a sward height of 50cm.

At the beginning of the experiment, the total number of species was counted and the canopy height measured at three random points in each plot. Comparison of these measurements between the different treatments showed that they did not differ significantly between uncut, partial cut and full cut plots at the start of the experiment (ANOVA, $p > 0.05$). From samples (0.25m²) of vegetation taken from the partial and full cut plots, it was estimated that an average of 1198gm⁻² of biomass (dry weight) was removed from partial cut treatments and 3100gm⁻² from full cut treatments. Comparison of these figures using ANOVA showed that significantly more biomass was removed from full cut treatments than partial cut treatments ($p > 0.05$).

On 14 November 2001 (51 days after treatment), the results of the experiment were collected by recounting the total number of species, measuring canopy height at three random points and taking total above ground biomass samples from a 0.25m x 0.25m quadrat in each plot. The biomass samples were separated into graminoid and forb portions which were dried and weighed.

4.3.2 Experiment 2: Effects of nutrient enrichment and protection from herbivores on growth of herbaceous vegetation on Mutum Island

Two enclosure experiments were set up on Mutum Island, which is located in the main channel of the Paraná, with the cooperation of a farmer who lives on the island and grazes cattle there. The area chosen for the first experiment was a regularly grazed, dry ridge, close to the farm. The vegetation was dominated by a low, prostrate, tough grass with few other species present. On 21 September 2001, eight 1m x 1m x 1m strong metal cages were positioned at random within an area of apparently homogeneous vegetation, approximately 80m by 40m, and firmly pegged into the ground at the corners. The 1m² plot underneath the enclosure constituted the protected (ungrazed) vegetation plot while 1m² on the east side of the enclosure (separated by 0.5m) was marked out as the unprotected (grazed) plot. The pairs of plots were assigned to two blocks and 15ml of Miracle Gro fertiliser (NPK 15:30:15 fertiliser with trace elements B, Cu, Fe, Mn and Zn) dissolved in water was applied to two pairs in each block. The remaining pairs were treated with the same volume of water to rule out the possibility that the application of water could be responsible for differences in the vegetation between plots. Protected and unprotected plots were positioned close together to maximise the similarity of vegetation being compared. However, this meant that fertiliser had to be applied to both plots, or neither, in a pair to avoid seepage of fertiliser into supposedly unfertilised plots. Four replicates were included due to the high risk of losing experimental units if the cattle damaged the enclosures.



Figure 4.3 Location of the first enclosure experiment on a dry ridge on Mutum Island

Vegetation responses were measured twice during this experiment. The first set of results was collected 53 days after treatment on 13 November 2001. Within each 1m^2 plot, all measurements were made in a central $0.5\text{m} \times 0.5\text{m}$ quadrat to avoid vegetation at the edges that may not have been so well protected from grazing (Figure 4.4). Canopy height was measured, and bare ground in a $0.1\text{m} \times 0.1\text{m}$ quadrat was estimated, each at three random points in the 0.25m^2 quadrat. The number of species was also counted and recorded. This quadrat was then divided into four 0.0625m^2 squares and one of these harvested as a biomass sample. The biomass sample was taken back to the laboratory where it was separated into graminoid and forb species and then dried for at least 48 hours until completely dry before weighing. After these samples had been collected, the exclosures were put back into place and left until 31 January 2002 (a total of 132 days after the experiment was begun) when the above measurements were repeated. The second biomass sample was taken from an area which had not been previously harvested.

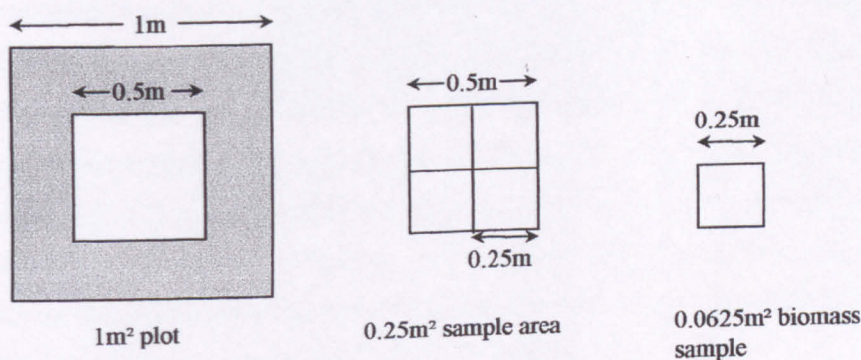


Figure 4.4 Experiment 2 sampling area

On 18 November 2002, a second exclosure experiment was set up in a contrasting environment. The exclosures were located on the same farm but this time they were arranged in a line along the edge of a lagoon, Lagoa do Geraldo. This area was at lower elevation and much wetter than the site of the previous experiment. The experimental plots were therefore influenced by the rising and falling water level of the lagoon, although it is believed that they did not become inundated during the course of the experiment. The proximity of the plots to the lagoon also made the open plots potentially more susceptible to trampling by the cattle as they moved to and from the lagoon to drink. As in the previous experiment, the vegetation in this area showed signs of intense grazing and was again dominated by a very short, creeping grass. The presence of an emergent wetland species, *Polygonum punctatum*, indicated the wetter condition of the soil here.



Figure 4.5 Lagoon shore enclosure experiment: Enclosure plot 1 and the adjacent unprotected plot with the semi-dry lagoon in the background.

The enclosures were arranged in a line parallel to the water's edge to try to keep the water table level similar between plots. The first four pairs of plots were assigned to block one and the second four pairs to block two so that differences in experimental field conditions along the line of plots might be detected. Figure 4.5 shows the positions of enclosure plot 1 and the adjacent unprotected plot in relation to the lagoon. The experiment was harvested after 74 days on 31 January 2003 using the same methods as in the January harvest of the previous experiment, except that the biomass sample consisted of the whole 0.25m² sampling area since only one harvest was made.

4.3.3 Data analysis

In all three experiments, three response variables were compared between treatments. These were the number of species (in 1m² in the cutting experiment and in 0.25m² in the enclosure experiments), canopy height, graminoid biomass, forb biomass, total biomass and the proportion of total biomass consisting of graminoid species (G:T). Each variable was tested for normality (Ryan-Joiner tests; $p > 0.05$) and for equal variance between groups to be compared (Levene's test; $p > 0.05$). Variables were normalised when possible by square root or natural log transformation. Normally distributed variables with equal variance between groups were tested for significant effects of enclosure treatment, fertiliser treatment, the interaction of these two treatments and experimental block using ANOVA. When response variables did not satisfy the assumptions of ANOVA, non-parametric tests were used to compare between treatments (Friedman or Kruskal Wallis

tests). Mean values were considered significantly different between treatments if $p \leq 0.05$. Statistical analyses were carried out using Minitab 13.30.



Figure 4.6 Looking along the line of exclosures positioned for the lagoon shore experiment

4.4 Results

4.4.1 Experiment 1: Impacts of disturbance (comparable to a single grazing event) on the structure of natural floodplain vegetation

Table 4.1 shows the mean or median values for each variable and reveals that species richness, canopy height and graminoid, forb and total biomass were all greater in uncut treatments than either of the cut treatments. However, the results of the ANOVA analyses and Friedman test showed that there were no statistically significant differences in any of the response variables between uncut, half cut and full cut plots after seven weeks regrowth (Table 4.1). The ratio of graminoid to total biomass was constant across the three treatments. There were also no significant differences in the response variables between blocks confirming that, although the vegetation was inherently variable, replicate plots could be realistically compared.

Table 4.1 Mean and standard error (S.e.) of normally distributed response variables (*median shown for G:T, the graminoid to total biomass ratio) in relation to cutting treatment, and significance of differences between treatments. Values were back-transformed where necessary to show original data.

Response	Uncut	S.e.	Half cut	S.e.	Full cut	S.e.	p
No. of species (in 0.25m ²)	5.33	0.88	3.67	0.88	3.67	0.33	0.164
Canopy height (m)	2.03	0.45	1.57	0.05	1.22	0.29	0.109
Graminoid biomass (g m ⁻²)	1934	857	1413	550	1306	812	0.859
Forb biomass (g m ⁻²)	47.8	47.1	24.7	19.3	23.9	15.9	0.989
Total biomass (g m ⁻²)	1982	836	1437	557	1330	826	0.850
*G:T	0.963		0.980		0.977		0.761

4.4.2 Experiment 2: Effects of protection from herbivores and nutrient enrichment on growth of herbaceous vegetation on Mutum Island

Dry ridge experiment: September 2001–January 2002

November: 53 days after treatment

The results of the analysis of variance showed that the response variables did not vary significantly due to block in November, indicating that the location of treatments did not affect the vegetation responses. Table 4.2 shows values of the response variables in relation to whether or not the vegetation was protected from grazing by an enclosure. Mean canopy height and total biomass were significantly greater in ungrazed plots than grazed plots. Graminoid biomass was greater in ungrazed than grazed plots, while percentage bare ground was greater in grazed than ungrazed plots but these differences were not significant. The proportion of total biomass contributed by graminoid species was similar in both levels of enclosure treatment.

Table 4.2 Mean and standard error (S.e.) of normally distributed response variables (*median shown for G:T) in November 2001 in relation to enclosure treatment, and significance of differences between treatments. Values are back-transformed where necessary to show original data.

Response	Ungrazed (exclosure)	S.e.	Grazed (no exclosure)	S.e.	p
No. of species (in 0.25 m ²)	6.25	0.65	5.50	0.80	0.505
Canopy height (m)	0.22	0.01	0.10	0.01	<0.001
Bare ground (%)	7.79	4.88	17.59	5.15	0.119
Graminoid biomass (g m ⁻²)	19.21	2.81	11.32	1.78	0.056
Forb biomass (g m ⁻²)	1.85	0.65	1.95	0.72	0.987
Total biomass (g m ⁻²)	21.05	2.56	13.28	1.51	0.040
*G:T	0.94		0.91		0.462

Most of the response variables had very similar mean values between the fertiliser treatments and so no significant effects of fertiliser treatment were detected (Table 4.3). Interaction between the two treatment factors also did not have a significant effect on any of the response variables.

Table 4.3 Mean and standard error (S.e.) of normally distributed response variables (*median shown for G:T) in November 2001 in relation to fertiliser treatment, and significance of differences between treatments. Values are back-transformed where necessary to show original data.

Response	+ Fertiliser	S.e.	- Fertiliser	S.e.	p
No. of species (in 0.25 m ²)	6.00	0.87	5.75	0.59	0.822
Canopy height (m)	0.17	0.02	0.14	0.03	0.152
Bare ground (%)	11.88	5.65	13.50	5.00	0.771
Graminoid biomass (g m ⁻²)	14.52	3.24	16.01	2.19	0.696
Forb biomass (g m ⁻²)	2.34	0.88	1.46	0.31	0.654
Total biomass (g m ⁻²)	16.86	2.86	17.46	2.23	0.654
*G:T	0.92		0.91		0.916

January: 132 days after treatment

In January, vegetation height was found to differ significantly between blocks one and two, illustrating the value of choosing a random block design which detects such differences, allowing them to be accounted for during analysis. None of the other response variables differed significantly between blocks.



Figure 4.7 Dry ridge exclosure experiment: Vegetation inside and surrounding the exclosure at plot 1 at the beginning of the experiment.

As in November, the exclosure treatment caused noticeable differences in the vegetation response variables. Figures 4.7 and 4.8 show the visible effects of one of the exclosures on the protected vegetation. At the start of the experiment, the vegetation was homogeneous inside and outside the exclosure (Figure 4.7), while at the end of the experiment, it was clear that there had been greater growth within the exclosure than outside it (Figure 4.8). The number of species in a plot, vegetation height, graminoid biomass, total biomass, and the ratio of graminoid biomass to total biomass, were all significantly greater in plots that had been protected by exclosures than in plots that had been accessible to cattle (Table 4.4).



Figure 4.8 Dry ridge enclosure experiment: Vegetation inside and surrounding the enclosure at plot 1 immediately before the final harvest of the experiment.

In ungrazed plots, forb biomass was lower and percentage bare ground was greater, but these differences were not significant. The results show a greater difference in the grazing treatments after 132 days than was apparent after 53 days.

Table 4.4 Mean and standard error (S.e.) of normally distributed response variables (*median shown for G:T) in January 2002 in relation to enclosure treatment and significance of differences between treatments. Values are back-transformed where necessary to show original data.

Response	Ungrazed (exclosure)	S.e.	Grazed (no exclosure)	S.e.	p
No. of species (in 0.25m ²)	5.25	0.45	3.75	0.45	0.040
Canopy height (m)	0.98	0.06	0.35	0.07	<0.001
Bare ground (%)	31.88	7.12	24.42	4.11	0.371
Graminoid biomass (g m ⁻²)	544.18	78.52	59.44	15.69	<0.001
Forb biomass (g m ⁻²)	16.18	4.55	29.04	5.23	0.092
Total biomass (g m ⁻²)	560.36	76.83	88.48	13.10	<0.001
*G:T	0.97		0.59		0.008



Figure 4.9 Measuring canopy height after removal of an exclosure in the dry ridge experiment.

Fertiliser application did not affect any of the response variables after 53 days or after 132 days (Table 4.5). The mean number of species, canopy height, graminoid biomass, forb biomass and total biomass were all very similar between fertiliser treatments. There was a greater percentage of bare ground and a greater contribution of graminoid species to total biomass in unfertilised plots compared to fertilised plots, but these differences were not significant. There were no significant effects of any interaction between the exclosure and fertiliser treatments.

Table 4.5 Mean and standard error (S.e.) of normally distributed response variables (*median shown for G:T) in January 2002 in relation to fertiliser treatment and significance of differences between treatments. Values are back-transformed where necessary to show original data.

Response	+ Fertiliser	S.e.	- Fertiliser	S.e.	p
No. of species (in 0.25m ²)	4.63	0.60	4.38	0.46	0.705
Canopy height (m)	0.69	0.13	0.64	0.15	0.588
Bare ground (%)	23.79	5.38	32.50	6.11	0.299
Graminoid biomass (g m ⁻²)	273.48	107.87	330.14	106.45	0.373
Forb biomass (g m ⁻²)	26.08	2.66	19.14	7.03	0.341
Total biomass (g m ⁻²)	299.56	106.24	349.53	102.45	0.377
*G:T	0.75		0.96		0.428

Lagoon shore: November 2002-January 2003

The response variables did not show any significant differences due to block, indicating that experimental conditions were similar within the study area. In concordance with the

observations in the previous experiment, application of fertiliser had no significant effect on any of the vegetation response variables measured (Table 4.6). The number of species present and mean vegetation height were very similar between the two treatments, while graminoid biomass and total biomass were slightly greater, and forb biomass was slightly lower, in fertilised treatments. The graminoid to total biomass ratio was very similar in both treatments.

Table 4.6 Mean and standard error (S.e.) of normally distributed response variables in January 2003 (* medians shown for non-normal variables) in relation to fertiliser treatment, and significance of differences between treatments. Values are back-transformed where necessary to show original data.

Response	+ Fertiliser	S.e.	- Fertiliser	S.e.	p
No. of species (in 0.25m ²)	5.00	0.73	4.00	0.57	0.311
Bare ground (%)	18.21	5.32	22.71	6.01	0.437
Graminoid biomass (g m ⁻²)	830.68	228.40	610.98	161.22	0.121
Total biomass (g m ⁻²)	835.63	228.75	616.05	160.16	0.132
*Forb biomass (g m ⁻²)	0.39		0.76		0.674
*Canopy height (m)	0.49		0.48		0.636
*G:T	0.999		0.998		0.598

Table 4.7 shows the effects of the exclosures on the response variables. Vegetation height, graminoid biomass and total biomass were all significantly greater inside exclosures than outside. Percentage bare ground was significantly lower inside exclosures than outside. The vegetation was clearly protected by the exclosures which prevented biomass removal and soil exposure. Forb biomass was low in all plots, (0-11% of the total biomass) and did not differ significantly between exclosure and open plots. The graminoid to total biomass ratio was consistent between treatments. The number of species in each plot ranged from one to seven and also did not differ significantly between exclosure and open plots.

There were no significant effects of interaction between the exclosure and fertiliser treatments on any of the response variables.

Table 4.7 Mean and standard error (S.e.) of normally distributed response variables in January 2003 (*medians shown for non-normal variables) in relation to exclosure treatment, and significance of differences between treatments. Values are back-transformed where necessary to show original data.

Response	Ungrazed (exclosure)	S.e.	Grazed (no exclosure)	S.e.	p
No. of species (in 0.25m ²)	4	0.78	5	0.50	0.311
Bare ground (%)	8.96	1.72	31.96	5.01	0.002
Graminoid biomass (gm ⁻²)	1079.40	207.54	362.26	43.77	<0.001
Total biomass (gm ⁻²)	1084.47	206.83	367.20	42.82	<0.001
*Forb biomass (gm ⁻²)	0.80		0.47		0.916
*Canopy height (m)	0.87		0.17		0.001
*G:T	0.999		0.998		0.461

4.5 Discussion

4.5.1 Experiment 1: Impacts of disturbance (comparable to a single grazing event) on the structure of natural floodplain vegetation

The results of the cutting experiment suggested that a single disturbance event, which might be caused by large herbivores passing through an area of vegetation, or in this case by cutting, did not damage the floodplain vegetation. At the end of the experiment (51 days after treatment), measurements of vegetation were similar between all plots whether they had been uncut, partially cut or cut to ground level. The cut vegetation therefore seemed to have regained the properties of the surrounding uncut vegetation which might be associated with its roles in supporting other organisms or providing a potential grazing resource. The tall canopy height and graminoid dominance over forbs were recovered, two factors important in the selection of vegetation by cattle (Clary & Leininger 2000; Quintana, Monge & Malvárez. 1998).

The wet grassland of the Baía floodplain appears to have the capacity to regenerate rapidly following major biomass removal. However, it is possible that frequent repetition of this kind of disturbance would give different results. Time limitations prevented the introduction of a second factor in the experiment investigating the effect of the frequency of such an impact. Although biomass can be considered one of the most representative response variables to grazing, it could be important to measure other responses of the

vegetation, such as stem density or stratified biomass. These responses could indicate changes in vegetation structure that might be important in habitat provision but which would not be detected by the simple measurements made in this experiment.

Although it has been shown that a single disturbance does not damage vegetation regrowth in the wet grassland where the experiment was conducted, the effects on drier areas of long-term, intense grazing, together with soil compaction impacts caused by trampling, are clear from the devegetated state of the islands in the river channel. Areas that have been grazed by moderate densities of cattle for decades show severely degraded vegetation of low biomass, sward height and species richness. The enclosure experiments were designed to provide some information on how this vegetation might develop if the pressure of cattle grazing was removed. Both experiments investigated the extremes of land use for cattle grazing purposes. The disturbance experiment showed the recovery of floodplain vegetation after a discrete disturbance event while the enclosure experiment illustrated the first stages in recovery from long-term intensive vegetation damage on the islands. The results of the cutting experiment indicate that it may be possible for some floodplain environments to support a level of cattle stocking which will not cause degradation of biomass and species richness and may therefore be compatible with a desire to maintain plant diversity and animal habitats. However, longer-term experiments would be required in order to make firm conclusions. It is possible that the várzea vegetation, which has become adapted during its evolution to withstand severe but occasional disturbance caused by floods or fire, may respond completely differently when exposed to continuous disturbance.

4.5.2 Experiment 2: Effects of protection from herbivores and nutrient enrichment on growth of herbaceous vegetation on Mutum Island

In the first enclosure experiment, after only seven weeks, plots that had been protected from grazing with enclosures had significantly greater canopy height and total biomass per unit area than plots which had been open to herbivores. However, the number of species in each plot, the percentage of bare ground and the graminoid and forb biomass per unit area were still similar in all plots, whether grazed or ungrazed. The vegetation was responding to the removal of the grazing pressure but was only at a very early stage of recovery. These initial results provide strong evidence that grazing is acting as a major control on the state of the vegetation in this area of Mutum Island. At the study site, it was known that

cattle were present and feeding on the vegetation. However, in other parts of the islands, cattle are not always observed but the similar appearance of the vegetation suggests that cattle are also influencing these areas.

By January 2002 (132 days after treatment), the more advanced stage of recovery of the vegetation was shown by significantly greater species richness, vegetation height, graminoid biomass, total biomass, and contribution of graminoid species to total biomass, in plots that had been protected from grazing. The dominant grass species recorded at the start of the experiment maintained its dominance, and showed its ability to accumulate biomass in the absence of herbivores. Under grazing pressure, this species grew to only a few centimetres in height but, with the protection of the exclosures, longer leaves were able to grow and survive. However, the significant increase in species richness suggested that the plant community was changing in response to removal of grazing disturbance. An increase in species richness following reduced disturbance is in accordance with the humpback model of species diversity (Grime 1973). The model predicts that species richness is low under severe disturbance or in the absence of any disturbance, and is maximised under a moderate level of disturbance. Under such intense grazing pressure, only a limited number of plant species can be expected to have adaptations to withstand the highly disturbed conditions. Removal of the disturbance and a subsequent increase in biomass could therefore be expected to encourage at least an initial increase in the number of species.

For the second experiment, the exclosures were put in place later in the season than for the first experiment. The increasingly favourable growth conditions leading into summer meant that plenty of growth took place during the shorter duration of the experiment so that in both years the vegetation was reaching the top of the exclosures (1m height) before it was harvested.

The results of both exclosure experiments showed that protection from grazing increased vegetation growth. However, there were some differences in the vegetation responses between the two experiments. The number of species per plot differed between exclosure and open plots in January 2002 but not in January 2003, while the percentage bare ground did not differ in 2002 but did in 2003.

The similarity in the number of species between exclosure and open plots in 2003 could suggest that grazing was not preventing colonisation by new species. However, in the first exclosure experiment, differences in species richness were not recorded when the

exclosures had been in place for only 53 days and only became apparent after 132 days. Perhaps the exclosures were not in place for a sufficiently long time (only 74 days) during the second experiment to stimulate changes in species richness. Alternatively, environmental stress, for example waterlogging and drying during the rise and fall of the water table, which could be expected to be closer to the soil surface in this experiment, may have been maintaining low diversity.

The difference in the effect of the exclosures on percentage bare ground may be explained by the different soil conditions at the two sites. The 2002-2003 experiment was located on the shore of a lagoon in a wetter area than in the previous experiment. The softer soil may have been more susceptible to poaching damage caused by the hooves of the cattle as they grazed, or drank from the lagoon. The disturbance caused by cattle poaching may have limited plant survival in areas that were not protected by exclosures. In the 2001-2002 experiment, the ground was drier and harder and so the hooves of the cattle did not sink into it. At this site, exclosures were situated at the side of a cattle path so cattle may only have trampled the open plots while grazing and used the path to move to other areas of the island. By the lagoon, cattle movement was not confined to pathways and the animals may have crossed the open plots while going to and from the water to drink, as well as while grazing.

The results of the exclosure experiments show the potential for recovery of currently intensively grazed vegetation on the islands in the Paraná channel. In both experiments, biomass increased dramatically in a few months and species diversity increased significantly in the drier vegetation, suggesting that a decrease in cattle stocking density could allow the vegetation to improve. In the second exclosure experiment, the graminoid proportion of total biomass also increased significantly. These changes could be of value to cattle farmers because cattle prefer to graze taller vegetation with a high graminoid component (Quintana, Monge & Malvárez 1998). A greater amount and diversity of vegetation is also of conservation value due to its role in providing spatially diverse habitats to support an increased diversity of other organisms.

No significant effects of fertiliser application were detected, possibly because the vegetation was not nutrient-limited, or because not enough fertiliser was applied to induce a significant increase in production. The increased level of flow regulation since Porto Primavera dam was completed in 1998 may have reduced the replenishment of soil nutrients by flood events. However, the droppings produced by the cattle may be

providing an alternative source of fertiliser for the vegetation if extra food from an outside source is fed to the animals.

4.6 Conclusions

- Canopy height and biomass of natural floodplain grassland vegetation can recover rapidly from a severe disturbance.
- Natural floodplain herbaceous vegetation may tolerate some level of exploitation as cattle pasture.
- Grazed island vegetation can rapidly regain biomass and height when herbivores are excluded.
- Prevention of grazing of island vegetation can result in increased species richness.
- Prevention of grazing can also reduce the area of bare ground.
- Intensive grazing may encourage growth of forb species rather than the Poaceae and Cyperaceae species most palatable to cattle.
- Management of grazing could potentially provide a more useful fodder resource and more diverse habitats for native organisms.
- Vegetation growth on the farm on Mutum Island does not appear to be nutrient-limited.

5 Effects of inter- and intra-specific competition and water nutrient availability on growth of floating aquatic plants

5.1 Aims

- To investigate the effects of different degrees of competition between pairs of floating aquatic plant species on their growth at two levels of nutrient availability.

5.2 Introduction

Current understanding of floodplain functioning suggests that the reduction in the extent and frequency of annual floods in the Paraná is likely to cause reductions in processes such as nutrient transport and recycling, dispersal of propagules and resetting of successional processes and diversification of habitats by erosion and sedimentation (Heiler *et al.* 1995; Junk, Bayley & Sparks 1989; Petts 1984; Thomaz, Roberto & Bini 1997; Ward & Stanford 1995). This alteration in the balance of stress (such as water nutrient availability) and disturbance (scouring and wash-out) can be expected to lead to alterations in plant community composition due to differences in the tolerance shown by individual species to the new conditions, and to their competitive interactions (Grime 1977).

Contrasting levels of sediment nitrogen and phosphorus (which could potentially become available to floating plants) between 2000-2001 TWINSPAN groups suggested that nutrient levels might influence species composition (Chapter Two, Section 2.4.2). The findings of the DCA and CCA analysis of the 2000-2001 data set supported this theory. Water phosphorus and sediment nitrogen were significantly correlated with site scores on axis two of the 2000-2001 DCA and CCA showed that sediment nitrogen and phosphorus were two of the best explanatory variables of species distributions (Chapter Two, Section 2.4.3). Water nitrogen was also significantly correlated with biomass (2000), sediment phosphorus with stem density (2000) and water phosphorus with leaf area (2001) (Chapter Two, Section 2.4.4).

A series of three glasshouse experiments was designed to examine the effects of the application of water nutrient and competition treatments on the growth of pairs of floating aquatic plant species. The species selected for study, *Salvinia auriculata* Aubl., *Pistia*

stratiotes L., and *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine, are prevalent in the floodplain and were observed, sometimes co-existing, at a number of sites during the field surveys conducted between 2000 and 2002.

5.3 Methods

Salvinia auriculata, *Pistia stratiotes* and *Limnobium laevigatum* (originally obtained from Glasgow Botanic Gardens) were placed in glasshouse culture and encouraged to grow and reproduce asexually between May and July 2001, in order to obtain sufficient plants to conduct experiments. Although the origins of the plants are unknown, it is likely that the original material was genetically identical and so the individuals produced through vegetative propagation for use in the experiment were also clones. This could be seen as a limitation of the experiment and a constraint on interpretation of the results, but in fact this is probably a genuine reflection of a lack of genetic diversity that could be expected in natural conditions. These three species readily and very rapidly reproduce asexually and so it is likely that plants within any particular waterbody will be closely related, if not genetically identical. Genetic similarity also provides another point of control over the experimental conditions meaning that any differences resulting between treatments are unlikely to be due to inherent differences in the plants themselves, but caused either by the factors being applied or by unintentional and uncontrolled differences in environmental conditions. The three species were cultured separately in 32L plastic tanks containing a mixture of sand and compost at the bottom and filled with tap water to which "Miracle-Gro" (NPK 15:30:15 fertiliser with trace elements B, Cu, Fe, Mn and Zn) was added periodically. During the long days of May, June and July, the plants grew rapidly in the greenhouse.

An identical experimental protocol was used in each of three experiments beginning with a study of the interaction between *Pistia* and *Salvinia*. *Pistia* and *Salvinia* plants were transferred into clean 32L tanks of tap water which contained a low concentration of nitrate but a high phosphate concentration at the source (Table 5.1). It was not possible to impose treatments of high and low water phosphorus concentration due to the difficulty in obtaining low phosphorus water (Table 5.1). Therefore, the two nutrient treatment levels consisted of i) water that was rich in phosphorus but poor in nitrogen and ii) water from the same source which had been supplemented with an NPK fertiliser. Competition and nutrient treatments were randomly assigned to tanks and the three replicates were arranged

in a random block design to help to reduce any potential effects of location within the greenhouse on plant growth (Figure 5.1).



Figure 5.1 Glasshouse experiment investigating competition between *Pistia stratiotes* and *Salvinia auriculata* at two levels of nutrient supply shortly before harvesting.

Competition treatments each consisted of a total plant density of eight plants per tank. At this density, the plants could interact but were not crowded for space until some growth had taken place under the treatment conditions. Five competition levels were set up consisting of different ratios of *Pistia* plants to *Salvinia* plants: 8:0, 6:2; 4:4; 2:6; 0:8. A *Pistia* plant was defined as one rosette with any daughter plants removed. *Salvinia* plants were approximately 5 to 10cm long with few or no branches. Plants were chosen for their similar size and shape in order to begin the experiment with conditions as similar as possible between treatments. After three days, nutrient treatments were imposed by the addition of "Miracle-Gro" solution to half of the tanks. The experiment therefore consisted of three replicates of a set of five competition treatments grown in tap water only, and an identical set of five competition treatments grown in tap water supplemented with 2.5ml of "Miracle-Gro" crystals per tank. The plants were left to grow in the greenhouse with a natural light supply and no heating from 20 July 2001. The tanks were topped up as necessary with tap water and no further fertiliser was added.

The experiment was harvested on 8 August 2001 when the plants had occupied all of the space in the growing tanks and conditions were becoming crowded enough for interaction to have taken place between the two species. Before harvesting, the number of *Pistia* individuals was counted and the proportion of the water surface area occupied by each species was estimated. Each species was collected separately from each treatment and

washed and oven-dried. Once dried to constant weight, total biomass per species for each experimental unit was recorded.

Table 5.1 Water quality at Garscube Estate, Switchback Road, Glasgow. (West of Scotland Water supply zone RB14).

Property	Value
Conductivity (mean)	61.4 μ S
pH (mean)	7.67
Reactive phosphate (minimum)	583 μ g/L
Nitrate (mean)	0.53mg/L
Calcium (minimum)	4.49mg/L
Potassium	<0.40mg/L

After this first harvest, the experiment was repeated following the same methods but with *Pistia* growing in combination with *Limnobium*. In this case it was easy to count individuals of both species as daughter plants were separated by floating stolons. This experiment was set up on 8 August 2001, fertiliser treatments were applied on 10 August 2001 and the plants were harvested on 9 October 2001. A third experiment following these methods was conducted between 3 May and 25 June 2002, investigating the interaction between *Salvinia* and *Limnobium*, to complete the study of pairwise competitive effects between the three floating plant species.

5.3.1 Data analysis

Total biomass per species and total biomass of both species in each competition treatment were used to plot replacement diagrams showing how the biomass of each of the species varied in both low and high nutrient treatments.

For each species, the response variables selected for comparison between treatments were total biomass, percentage canopy cover, final number of plants, biomass per initial plant, biomass per unit canopy cover and biomass per final plant. *Salvinia* plants could not be counted without fragmenting and so the final number of plants and biomass per final plant could not be measured. Normality of the response data was examined using Ryan-Joiner tests. The data were considered normal if $p \geq 0.05$. Most variables were normally distributed or could be normalised by square root or natural log transformation. Levene's test showed that all normally distributed variables had equal variance between groups to be compared ($p \geq 0.05$).

The response variables with normal distribution and equal variance in groups were analysed for statistically significant differences due to treatment factors using ANOVA. Tukey's multiple comparisons showed which experimental treatments were responsible for the differences.

The data for two of the plant response variables could not be made normal by transformation and so ANOVA could not be applied. These variables were *Pistia* percentage cover in the *Pistia-Salvinia* experiment and *Salvinia* yield per initial plant in the *Limnobium-Salvinia* experiment. In order to separate the effects of fertiliser and competition, in each case the data were split into two sets, one of fertilised treatments and the other of unfertilised treatments. A two-way ANOVA or a Friedman two-way analysis of variance and a multiple comparison test (Siegel & Castellan 1988, pp.180-181) (normal or non-normal data sub-sets respectively) were used to investigate responses to competition, taking account of the block design of the experiment. Kruskal-Wallis tests were used to compare effects of fertiliser application in both experiments. All statistical analyses were carried out using Minitab 13.30.

Following comparison of species responses between experimental treatments, values for relative yields, relative yield totals (de Wit & van den Bergh 1965; Martin & Snaydon 1982) and aggressivity scores (McGilchrist & Trenbath 1971) were calculated for each pair of interacting species. These numbers describe how two species interact with each other and whether or not they impose competitive effects on each other.

The relative yield of species i compares its yield per initial plant when it is growing in mixture with species j , with its yield when it is growing only with other individuals of species i (Equation 5.1). If this value is greater than one, species i shows an increase in yield in response to growing in mixture compared to growing alone. If it is less than one, the yield of species i is reduced by interaction with species j compared to its yield when growing alone.

Equation 5.1

Relative yield of species $i = Y_{ij} / Y_{ii}$

Y_{ij} = yield of species i per initial plant when grown in mixture with species j .

Y_{ii} = yield of species i per initial plant when grown only with other individuals of the same species.

A relative yield total (RYT) (de Wit & van den Bergh 1965; Martin & Snaydon 1982) can be calculated for two species growing in a one to one ratio mixture in order to describe the effect on combined yield of mixing the species (Equation 5.2). If the RYT for a pair of species is close to one, then the combined yield per plant for the two species is similar whether they are growing together or separately. This may be because neither shows a difference in yield, or because one shows an increase and the other a decrease. If the RYT is greater than one, then the overall effect of mixing the two species is an increase in yield per individual. Conversely, if RYT is less than one then mixing the two species causes a decrease in overall yield per plant.

Equation 5.2

$$\text{Relative yield total} = \frac{1}{2} (Y_{ij}/Y_{ii} + Y_{ji}/Y_{jj})$$

The relationship of the yields of the two species can be described by the aggressivity score (McGilchrist & Trenbath 1971) of one relative to the other (Equation 5.3). If the aggressivity score is large, the yield of species *i* is either being reduced less, or increased more, than species *j* when the two species are mixed compared to when they are not. It can therefore be considered more aggressive in the competitive interaction as it is being more successful than species *j* by either increasing its yield above what would be expected in pure culture, or minimizing a reduction in yield due to mixing.

Equation 5.3

$$\text{Aggressivity of species } i \text{ relative to species } j = \frac{1}{2}(Y_{ij} / Y_{ii} - Y_{ji} / Y_{jj})$$

5.4 Results

5.4.1 Replacement diagrams

Figure 5.2 illustrates the biomass yields obtained per species in each of the plant density combinations and fertiliser treatments applied to *Pistia* and *Salvinia*. The same pattern was observed in both fertilised and unfertilised treatments with biomass always slightly greater in fertilised treatments. Biomass yield per species was proportional to the number of individuals of that species present at the start of the experiment, and was greater in all cases where fertiliser was applied. Total biomass yield per experimental unit was proportional to the number of *Pistia* individuals and inversely proportional to the number

of *Salvinia* individuals present at the beginning of the experiment. Biomass yields became equivalent in the two species when six *Salvinia* plants were grown with two *Pistia* plants.

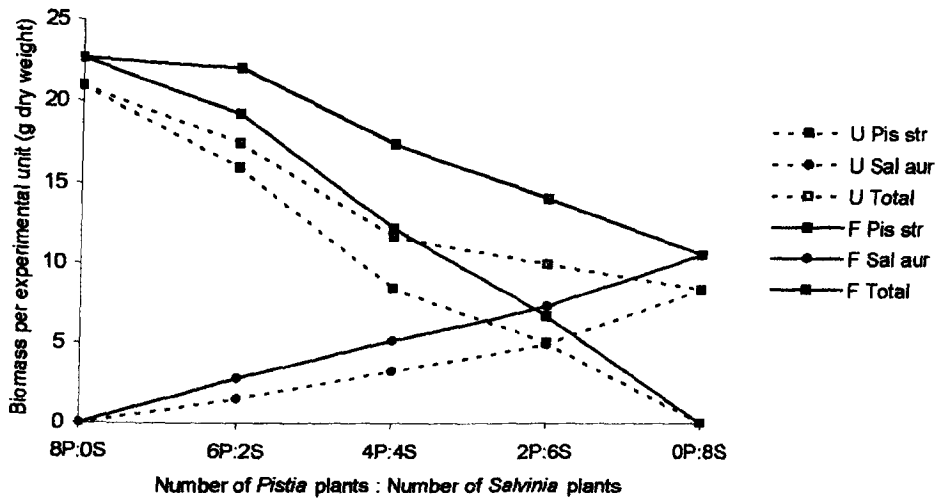


Figure 5.2 Replacement diagram for interaction of *Pistia stratiotes* (P; filled squares) and *Salvinia auriculata* (S; filled circles) growing alone and in combination in varying densities, treated with fertiliser (F; unbroken line) or untreated (U; broken line). Total biomass yield per experimental unit is shown by open squares.

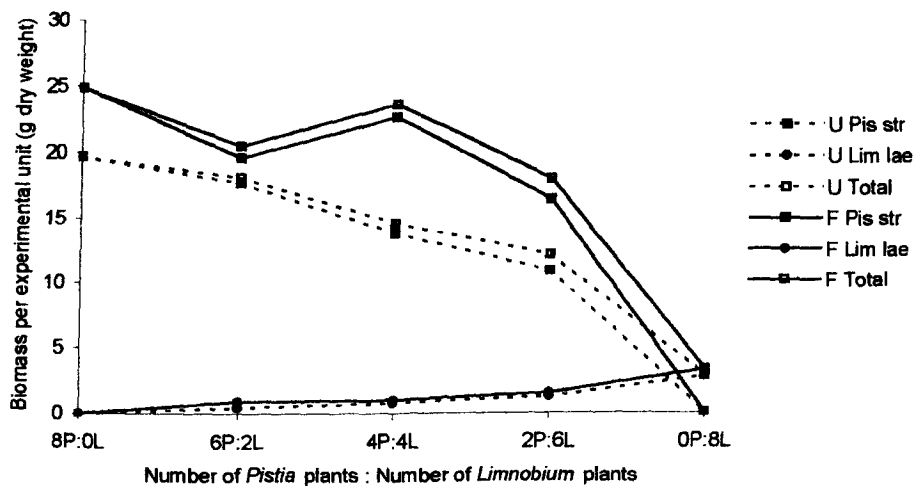


Figure 5.3 Replacement diagram for interaction of *Pistia stratiotes* (P; filled squares) and *Limnobium laevigatum* (L; filled circles) growing alone and in combination in varying densities, treated with fertiliser (F; unbroken line) or untreated (U; broken line). Total biomass yield per experimental unit is shown by open squares.

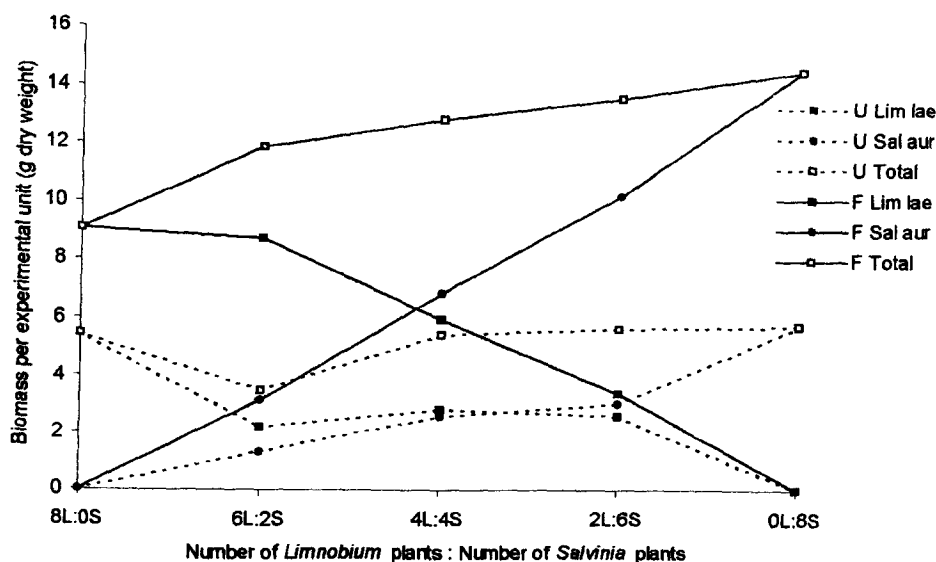


Figure 5.4 Replacement diagram for interaction of *Limnobium laevigatum* (L; filled squares) and *Salvinia auriculata* (S; filled circles) growing alone and in combination in varying densities, treated with fertiliser (F; unbroken line) or untreated (U; broken line). Total biomass yield per experimental unit is shown by open squares.

Results of the interaction of *Pistia* with *Limnobium* were also dominated by the greater size of *Pistia*. In unfertilised treatments, biomass yield per species was proportional to the starting density of that species, although this response was more conspicuous in *Pistia* than *Limnobium* (Figure 5.3). Total biomass was in this case proportional to the number of *Pistia* plants and inversely proportional to the number of *Limnobium* plants, which made little contribution to total biomass. In fertilised treatments, the pattern was affected by particularly high *Pistia* biomass in the four *Pistia* : four *Limnobium* treatment. Apart from this result, yield per species was proportional to the respective starting density, and total yield to the starting density of *Pistia*. Figure 5.3 shows the limited success of *Limnobium* and its lack of competitive ability relative to *Pistia*.

In the interaction of *Limnobium* and *Salvinia* under fertilised conditions, mean total biomass per experimental unit increased as the proportion of *Salvinia* individuals increased (Figure 5.4). Biomass of *Limnobium* per unit was similar between treatments with eight and six *Limnobium* individuals but declined at lower densities. *Salvinia* biomass increased approximately linearly as its density increased. *Salvinia* and *Limnobium* biomass were very similar when the species were mixed in equal numbers. A different pattern of biomass was observed in the unfertilised treatments. Total biomass did not show a clear trend across the treatments but was similar at each species density, except when six *Limnobium* were grown with two *Salvinia* when it was reduced. *Limnobium* biomass was greatest in the absence of *Salvinia* but did not show a consistent decline as *Salvinia* density

increased. Instead it was similar in all three mixtures with *Salvinia*. In contrast, *Salvinia* biomass increased with each increase in its density relative to *Limnobium*.

5.4.2 Analysis of treatment effects

Pistia v *Salvinia*

Salvinia total biomass, yield per initial plant and biomass per unit area were significantly greater in fertilised than in unfertilised treatments (Table 5.2). Percentage cover was similar between fertiliser treatments. In fertilised treatments, *Salvinia* reached greater levels of biomass using the same water surface area by changing leaf orientation from a horizontal position to a vertical position and building up layers of plants once there was no further surface space available. The fragility of the plants made it impossible to count numbers of individuals but the formation of layers of plants suggests an increase in the size or number of plants, or both.

Table 5.2 Responses of *Pistia stratiotes* and *Salvinia auriculata* to fertiliser treatments (-F no fertiliser; +F fertiliser added). Mean values for normal response variables (back-transformed where necessary to show original values) are given with standard errors in brackets and the p-value for the significance of differences between competition levels. The median is quoted for *Pistia* % cover. (g dw = grams dry weight).

Response variable	<i>Pistia stratiotes</i>			<i>Salvinia auriculata</i>		
	- F	+ F	p	- F	+ F	p
Biomass (g dw)	12.64 (1.94)	15.27 (2.03)	0.016	4.56 (0.81)	6.53 (0.95)	0.001
% cover	42.5	75.00	0.038	52.08 (8.52)	49.6 (10.9)	0.522
Final number of plants	8.58 (1.00)	26 (3.33)	<0.001			
Yield per initial plant (g dw)	2.50 (0.11)	3.09 (0.13)	<0.001	0.87 (0.05)	1.18 (0.09)	0.005
Biomass per unit area (g dw)	0.25 (0.01)	0.21 (0.02)	0.018	0.09 (0.01)	0.24 (0.08)	<0.001
Biomass per final plant (g dw)	1.47 (0.15)	0.64 (0.07)	<0.001			

Salvinia biomass and percentage cover were significantly different between all competition treatments, increasing with the initial number of *Salvinia* plants in the treatment (Table 5.3). *Salvinia* yield per initial plant did not show any significant differences due to

competition. *Salvinia* biomass per unit final canopy area was significantly greater in the treatment with only two *Salvinia* plants than in the other treatments with more *Salvinia* plants (Table 5.3). None of the *Salvinia* response variables differed significantly between blocks.

Tables 5.3 and 5.4 Responses of *Pistia stratiotes* (P) and *Salvinia auriculata* (S) to competition treatments. Mean values for normal response variables (back-transformed where necessary to show original values) are given with standard errors in brackets and the p-value for the significance of differences between competition levels. The median is quoted for *Pistia* % cover. Significantly different results are labelled with different letter codes while those sharing the same letter are not significantly different. (g dw = grams dry weight).

Table 5.3 *Salvinia* responses to competition with *Pistia*.

Response variable	6P:2S	4P:4S	2P:6S	0P:8S	p
Biomass(g dw)	2.17 ^a (0.70)	4.24 ^b (0.55)	6.20 ^c (0.62)	9.58 ^d (0.65)	<0.001
% cover	9.17 ^a (2.01)	39.17 ^b (4.17)	60.83 ^c (6.38)	94.17 ^d (2.71)	<0.001
Yield per initial plant (g dw)	0.85 (0.12)	1.06 (0.14)	0.99 (0.11)	1.20 (0.08)	0.107
Biomass per unit area (g dw)	0.34 ^a (0.16)	0.12 ^b (0.02)	0.11 ^b (0.02)	0.10 ^b (0.004)	0.002

Table 5.4 *Pistia* responses to competition with *Salvinia*.

Response variable	8P:0S	6P:2S	4P:4S	2P:6S	p
Biomass (g dw)	21.78 ^a (1.22)	17.66 ^b (1.82)	10.44 ^c (0.92)	5.94 ^d (0.45)	<0.001
% cover (+F)	90 ^a	85 ^{ab}	70 ^{ab}	30 ^b	0.046
% cover (-F)	80 ^a	70 ^{ab}	30 ^{ab}	25 ^b	0.029
Final number of plants	24.33 ^a (6.61)	21.00 ^a (4.39)	16.33 ^a (3.90)	7.50 ^b (1.95)	<0.001
Yield per initial plant (g dw)	2.72 (0.15)	3.13 (0.25)	2.61 (0.23)	2.72 (0.17)	0.062
Biomass per unit area (g dw)	0.25 (0.01)	0.24 (0.02)	0.25 (0.03)	0.20 (0.02)	0.094
Biomass per final plant (g dw)	1.35 (0.34)	1.06 (0.24)	0.82 (0.17)	0.98 (0.16)	0.108

Like *Salvinia*, *Pistia* biomass increased with the initial number of *Pistia* plants and was significantly different between all treatments (Table 5.4). The final number of *Pistia* plants was similar except in the lowest starting density treatment which produced significantly fewer plants. Percentage cover increased with initial *Pistia* density in both fertilised and unfertilised treatments and was significantly greater in the treatment that began with eight *Pistia* plants than in the treatment that began with two *Pistia* plants. There were no significant effects of competition on *Pistia* yield per initial plant, biomass per unit canopy area or biomass per final individual (Table 5.4).

Pistia total biomass, total percentage cover, final number of plants and yield per initial plant were all significantly greater in fertilised than unfertilised treatments (Table 5.2). Biomass per unit area and biomass per final plant were lower in fertilised than unfertilised treatments. The greater weight per *Pistia* plant in unfertilised treatments was explained by the three-fold increase in the number of *Pistia* plants in fertilised treatments compared to unfertilised treatments and parallel but only slight increase in total *Pistia* biomass (Table 5.2). This shows that fertiliser addition favoured vegetative reproduction rather than encouraging an increase in individual plant size. Like biomass per final individual, biomass per unit final canopy area was also greater in the absence of fertiliser, as the additional nutrients in fertilised treatments appeared to be invested in expansion across the water surface by the new plants, rather than in building up biomass of existing plants.

Pistia biomass, yield per initial plant and biomass per unit canopy area differed significantly between blocks but this source of variation was accounted for in the ANOVA design.

Pistia* v *Limnobium

Mean *Pistia* biomass and percentage cover were significantly greater when this species was grown alone than in the treatment with its lowest density relative to *Limnobium* (Table 5.5). The final number of *Pistia* plants was significantly greater in the treatments with an initial density of six or eight *Pistia* plants than with two *Pistia* plants. *Pistia* yield per initial plant increased significantly as the initial number of *Pistia* plants decreased and the initial number of *Limnobium* plants increased (Table 5.5). *Pistia* biomass per final plant and biomass per unit final canopy area did not vary in response to competition level (Table 5.5).

Tables 5.5 & 5.6 Responses of *Pistia stratiotes* (P) and *Limnobium laevigatum* (L) to competition treatments. Mean values for normal response variables (back-transformed where necessary to show original data) are given with standard errors in brackets and the p-value for the significance of differences between competition levels. Significantly different results are labelled with different letter codes while those sharing the same letter are not significantly different.

Table 5.5 *Pistia* responses to competition with *Limnobium*.

Response variable	8P:0L	6P:2L	4P:4L	2P:6L	p
Biomass (g dw)	22.26 ^a (1.40)	18.58 ^{ab} (1.20)	18.21 ^{ab} (2.40)	13.65 ^b (2.54)	0.009
% cover	85.83 ^a (6.11)	76.67 ^{ab} (5.73)	64.2 ^{ab} (10.9)	55.0 ^b (12.9)	0.006
Final number of plants	24.33 ^a (5.68)	24.0 ^a (5.26)	19.50 ^{ab} (4.63)	14.83 ^b (3.79)	0.007
Yield per initial plant (g dw)	2.78 ^a (0.18)	3.10 ^{ab} (0.20)	4.55 ^{bc} (0.60)	6.83 ^c (1.27)	<0.001
Biomass per unit area (g dw)	0.26 (0.01)	0.25 (0.02)	0.31 (0.03)	0.29 (0.05)	0.382
Biomass per final plant (g dw)	1.17 (0.22)	0.99 (0.23)	1.11 (0.15)	1.37 (0.45)	0.443

Table 5.6 *Limnobium* responses to competition with *Pistia*.

Response variable	6P:2L	4P:4L	2P:6L	0P:8L	p
Biomass (g dw)	0.37 ^a (0.10)	0.88 ^{ab} (0.20)	1.41 ^b (0.27)	3.06 ^c (0.61)	<0.001
% cover	4.00 ^a (0.45)	9.17 ^a (2.44)	13.33 ^{ab} (3.07)	30.83 ^b (9.95)	0.001
Final number of plants	2.83 ^a (0.60)	6.50 ^{ab} (1.09)	9.50 ^b (0.96)	15.00 ^c (1.06)	<0.001
Yield per initial plant (g dw)	0.19 (0.05)	0.22 (0.05)	0.24 (0.05)	0.38 (0.08)	0.163
Biomass per unit area (g dw)	0.10 (0.03)	0.10 (0.02)	0.14 (0.03)	0.11 (0.01)	0.677
Biomass per final plant (g dw)	0.13 (0.04)	0.13 (0.02)	0.14 (0.01)	0.21 (0.04)	0.196

Mean *Pistia* biomass, percentage cover, final number of plants and yield per initial plant were all significantly greater in fertilised treatments than in unfertilised treatments (Table 5.7). Biomass per final plant and biomass per unit final canopy area were significantly lower in fertilised treatments than in unfertilised treatments (Table 5.7), as was observed in

the *Pistia-Salvinia* experiment (Table 5.2). Biomass per initial plant differed significantly between blocks but this effect was accounted for in the ANOVA design.

Limnobium biomass, percentage cover and final number of plants tended to increase as the initial number of *Limnobium* plants increased with significant differences between some of the treatments (Table 5.6). However, there was no significant effect of fertiliser addition on these response variables (Table 5.7).

Analysis of variance of *Limnobium* yield per initial plant, biomass per final plant and biomass per unit final canopy area showed that there were no significant effects of either treatment factor or of block (Table 5.6 and Table 5.7).

Table 5.7 Responses of *Pistia stratiotes* and *Limnobium laevigatum* to fertiliser treatments (-F no fertiliser; +F fertiliser added). Mean values for normal response variables (back-transformed where necessary to show original values) are given with standard errors in brackets and the p-value for the significance of differences between competition levels.

Response variable	<i>Pistia stratiotes</i>			<i>Limnobium laevigatum</i>		
	- F	+ F	p	- F	+ F	p
Biomass (g dw)	15.5 (1.52)	20.85 (1.28)	0.003	1.32 (0.29)	1.54 (0.46)	0.822
% cover	53.33 (6.58)	87.50 (3.11)	<0.001	10.83 (2.13)	17.83 (6.15)	0.390
Final number of plants	10.42 (1.09)	30.92 (2.05)	<0.001	8.42 (1.25)	8.50 (1.69)	0.936
Yield per initial plant (g dw)	3.58 (0.59)	5.05 (0.69)	0.001	0.24 (0.03)	0.27 (0.06)	0.918
Biomass per unit area (g dw)	0.31 (0.02)	0.24 (0.01)	0.006	0.13 (0.02)	0.10 (0.01)	0.251
Biomass per final plant (g dw)	1.63 (0.19)	0.69 (0.04)	<0.001	0.14 (0.01)	0.17 (0.03)	0.561

Limnobium* v *Salvinia

Mean *Limnobium* biomass, percentage cover and final number of plants increased as the initial number of *Limnobium* plants increased (Table 5.8). Yield per initial plant and biomass per unit canopy area were significantly greater in the lowest *Limnobium* density than in the two highest density treatments. Biomass per final plant did not differ significantly between competition treatments.

Table 5.8 & Table 5.9 Responses of *Limnobium laevigatum* (L) and *Salvinia auriculata* (S) to competition treatments. Mean values (back-transformed where necessary to show original data) for normal response variables are given with standard error in brackets and the p-value for the significance of differences between competition levels. The median is quoted for *Salvinia* yield per initial plant (-F). Significantly different results are labelled with different letter codes while those sharing the same letter are not significantly different.

Table 5.8 *Limnobium laevigatum* responses to competition with *Salvinia auriculata*.

Response variable	8L:0S	6L:2S	4L:4S	2L:6S	p
Biomass (g dw)	7.25 ^a (1.06)	5.47 ^a (1.52)	4.43 ^b (0.71)	2.99 ^b (0.41)	<0.001
% cover	47.50 ^a (9.64)	32.50 ^{ab} (8.34)	22.50 ^{bc} (4.43)	10.83 ^c (2.01)	<0.001
Final number of plants	32.00 ^a (5.85)	24.83 ^b (6.07)	18.17 ^b (3.53)	11.67 ^c (2.36)	<0.001
Yield per initial plant (g dw)	0.908 ^a (0.133)	0.913 ^a (0.254)	1.108 ^{ab} (0.178)	1.500 ^b (0.205)	0.015
Biomass per unit area (g dw)	0.168 ^a (0.019)	0.180 ^a (0.043)	0.210 ^{ab} (0.028)	0.313 ^b (0.045)	0.017
Biomass per final plant (g dw)	0.235 (0.014)	0.208 (0.024)	0.253 (0.012)	0.287 (0.043)	0.075

Table 5.9 *Salvinia auriculata* responses to competition with *Limnobium laevigatum*.

Response variable	6L:2S	4L:4S	2L:6S	0L:8S	p
Biomass (g dw)	2.24 ^a (0.42)	4.74 ^b (1.00)	6.63 ^c (1.71)	10.15 ^d (2.02)	<0.001
% cover	16.67 ^a (3.80)	40.00 ^b (9.31)	55.00 ^b (9.13)	73.3 ^c (10.9)	<0.001
Yield per initial plant (-F) (g dw)	0.650	0.670	0.530	0.700	0.167
Yield per initial plant (+F) (g dw)	1.587 (0.096)	1.723 (0.142)	1.703 (0.174)	1.817 (0.115)	0.308
Biomass per unit area (g dw)	0.152 (0.022)	0.120 (0.005)	0.112 (0.014)	0.137 (0.013)	0.239

Salvinia biomass and percentage cover increased as the initial number of *Salvinia* plants increased (Table 5.9). In contrast with *Limnobium*, the yield per initial plant of *Salvinia* did not differ significantly between competition treatments in fertilised or unfertilised treatments (Table 5.9). Biomass per unit area was not significantly different between competition treatments. *Salvinia* biomass differed significantly between blocks but this source of variation was accounted for in the ANOVA design.

Table 5.10 Responses of *Limnobium laevigatum* and *Salvinia auriculata* to fertiliser treatments (-F no fertiliser; +F fertiliser added). Mean values for normal response variables (back-transformed where necessary to show original data) are given with standard errors in brackets and the p-value for the significance of differences between treatments. The median is quoted for *Salvinia* yield per initial plant.

Response variable	<i>Limnobium laevigatum</i>			<i>Salvinia auriculata</i>		
	- F	+ F	p	- F	+ F	p
Biomass (g dw)	2.62 (0.49)	5.44 (0.96)	<0.001	2.54 (0.53)	6.96 (1.39)	<0.001
% cover	13.33 (2.79)	32.00 (6.74)	<0.001	22.67 (4.95)	51.33 (9.35)	<0.001
Final no. of plants	9.93 (1.82)	24.73 (4.35)	<0.001			
Yield per initial plant (g dw)	0.61 (0.12)	1.16 (0.18)	<0.001	0.65	1.59	<0.001
Biomass per final plant (g dw)	0.22 (0.04)	0.18 (0.03)	0.021			
Biomass per unit area (g dw)	0.19 (0.04)	0.16 (0.03)	0.139	0.10 (0.02)	0.11 (0.02)	0.817

The addition of fertiliser to the experimental units caused a highly significant increase in percentage cover, final number of plants, total biomass and yield per initial plant of *Limnobium* relative to unfertilised treatments (Table 5.10). Biomass per final plant was significantly greater in unfertilised than fertilised treatments. This illustrates that *Limnobium* responded to high nutrient conditions by producing large numbers of daughter plants which were lightweight in comparison to plants growing in poorer nutrient conditions. However, both distributions of biomass, in either a few large plants or many small plants, resulted in similar biomass per unit area.

Salvinia also responded to higher nutrient conditions with significantly greater percentage cover, biomass and yield per initial plant (Table 5.10). Biomass per unit area did not differ significantly between treatments.

5.4.3 Relative yields, relative yield totals and aggressivity scores

The relative yields of *Pistia* and *Salvinia* in combination were very similar to each other in both fertilised and unfertilised experimental conditions (Table 5.11). The figures of less than one in unfertilised treatments show that there was a greater yield per plant in both species when they were grown alone than when they were grown in mixture. Mixing

Pistia with *Salvinia* suppressed the yield per plant compared to the yield that could be expected from plants grown in single species units. However, for fertilised treatments, the relative yields of both *Pistia* and *Salvinia* were close to one showing that this suppression did not occur in the more nutrient-enriched conditions (Table 5.11). As both species responded to interaction in the same way, the relative yield total did not provide any more information than the individual relative yields (Table 5.12). When nutrients were in plentiful supply (particularly nitrogen, which was low in unfertilised treatments), it made no difference to the yield of the plants whether they were grown in mixture or not. However, under limited nutrient supply, competition between the two species caused a reduction in yield per individual relative to the yield obtained from single species cultures at the same plant density.

The relative yield of *Pistia* in mixed culture with *Limnobium* was greater than one and increased further when calculated from fertilised treatments (Table 5.11) indicating that mixing substantially increased yield and the addition of fertiliser caused a further increase. The relative yield of *Limnobium* was similar whether or not fertiliser was added, and suggested a reduction in yield per plant in response to mixing although yield per plant did not differ significantly between competition treatments when tested with ANOVA. The relative yield total for the two species without fertiliser showed that mixing had no effect on their combined yield per plant (Table 5.12). The opposing responses of *Pistia*, which had a greater yield in mixture, and *Limnobium*, which had a lower yield, resulted in a relative yield total close to one. The addition of fertiliser increased the relative yield total to a value greater than one, which indicated a combined response to mixing of an increase in yield.

Table 5.11 Relative yields of *Pistia stratiotes*, *Limnobium laevigatum* and *Salvinia auriculata*.

Interaction	Species	Relative Yield	
		Unfertilised	Fertilised
<i>Pistia</i> v <i>Salvinia</i>	<i>Pistia</i>	0.81	1.09
	<i>Salvinia</i>	0.77	0.97
<i>Pistia</i> v <i>Limnobium</i>	<i>Pistia</i>	1.41	1.82
	<i>Limnobium</i>	0.54	0.60
<i>Limnobium</i> v <i>Salvinia</i>	<i>Limnobium</i>	1.06	1.33
	<i>Salvinia</i>	0.95	0.90

Relative yields of *Limnobium* and *Salvinia* differed from each of the other two pairings of species. In this interaction, under unfertilised conditions mixing the species had a minimal

influence on their yields. In fertilised conditions, *Limnobium* growth was enhanced by mixing with *Salvinia* compared to its growth alone, while the *Salvinia* plants responded to mixing with a slight reduction in yield. The relative yield total for the two species was slightly greater than one, indicating that their combined biomass yield was greater when they were grown together than independently. This was not the case in unfertilised treatments where the relative yield total was almost equal to one, indicating that combined yield was not affected by whether the plants were grown in single or mixed species units.

Table 5.12 Relative yield totals and aggressivity scores for pairwise interactions of *Pistia stratiotes*, *Salvinia auriculata* and *Limnobium laevigatum*.

Species mixture	Aggressivity score		Relative Yield Total	
	Unfertilised	Fertilised	Unfertilised	Fertilised
<i>Pistia</i> v <i>Salvinia</i>	0.02	0.06	0.79	1.03
<i>Pistia</i> v <i>Limnobium</i>	0.43	0.61	0.98	1.21
<i>Limnobium</i> v <i>Salvinia</i>	0.06	0.22	1.01	1.12

The positive aggressivity score for *Pistia* in relation to *Limnobium* grown without fertiliser addition indicates that *Pistia* benefited more from the interaction than *Limnobium*, with a greater increase in yield per plant. The aggressivity score for *Pistia* was increased by the addition of fertiliser to experimental units. The greater supply of nutrients made *Pistia* even more aggressive relative to *Limnobium*.

In the case of the *Pistia* and *Salvinia* combination, the very similar responses of the two species to interaction in both fertilised and unfertilised treatments resulted in aggressivity scores for *Pistia* relative to *Salvinia* of close to zero. Neither of these two species had a negative effect on the other.

The absence of an effect of *Limnobium* on *Salvinia* growth in unfertilised treatments is shown by the aggressivity score close to zero. However, in fertilised treatments, the aggressivity of *Limnobium* towards *Salvinia* was found to be greater than one, indicating that *Limnobium* benefited more from the interaction than *Salvinia*.

5.5 Discussion

In the *Pistia* - *Salvinia* experiment, biomass yields of both *Salvinia* and *Pistia* per initial plant were increased by the addition of fertiliser. The plants with increased availability of nitrogen, phosphorus and micronutrients accumulated biomass more rapidly than those in

unfertilised conditions (high in phosphorus but low in other nutrients). Mixing the two species in unfertilised conditions caused a slight reduction in their yields but this effect was removed by the addition of fertiliser.

The greater biomass per unit final canopy area of *Salvinia* in fertilised conditions than unfertilised conditions shows that its biomass was not entirely limited by space because new growth could form layers on top of other plants. In unfertilised treatments, increased densities of *Pistia* relative to *Salvinia* also resulted in greater biomass per unit canopy area of *Salvinia*. This could be due to large *Pistia* plants forcing the *Salvinia* plants into smaller areas where they continued to accumulate biomass but were unable to expand laterally. However, in fertilised treatments, *Salvinia* biomass per unit canopy area was unaffected by the proportions of the two species. Fertiliser addition had an opposite effect on *Pistia*, which showed reduced biomass per unit canopy area and per final individual in fertilised compared with unfertilised treatments. This was due to rapid generation of new individuals in response to increased nutrients. There was therefore a substantial increase in the area occupied by the species but the increase in biomass was not of the same magnitude. High nutrient conditions could be expected to cause an initial reduction in the density of *Pistia* biomass in a water body. However, the resulting explosion in the number of propagules could help to encourage the dispersal of the species into connected habitats. This response could be considered an evolutionary adaptation to the floodpulses common in the floodplain habitats in which *Pistia* is native. Flood events tend to cause an increase in water nutrients and at the same time increase connectivity between aquatic habitats. By responding to the rise in nutrients with an increase in the production of daughter plants, the potential for *Pistia* to reach and colonise new habitats is increased.

In the *Pistia* - *Limnobium* experiment, *Limnobium* plants appeared to grow more successfully alone than if they were forced to interact with strongly aggressive *Pistia*, although comparisons between competition treatments were not statistically significant. *Pistia* yielded more biomass per initial plant if it was grown in mixture with *Limnobium* rather than with further individuals of its own species. In this combination, intraspecific competition had more influence on *Pistia* success than interspecific competition. The relatively small and non-aggressive *Limnobium* plants made more benign neighbours than other *Pistia* individuals which took up more space and presumably consumed more nutrients due to their tendency for fast growth and proliferation. The contrast in success of the two species therefore may have resulted more from the flourishing of *Pistia* under conditions of low intraspecific competition than the suppression of *Limnobium* by interspecific competition from *Pistia*.

When nutrients were in greater supply, *Pistia* was able to take advantage of the favourable conditions in the species mixture treatments and showed even greater increases in yield compared to single species units. The provision of additional nutrients did not encourage *Limnobium* growth in single species or competition treatments, suggesting a poor competitive capacity. Both experiments with *Pistia* demonstrate the ability of this species to produce propagules rapidly in response to the addition of fertiliser. The additional plants generated may provide it with more expansive root and leaf systems which allow it to exploit the improved nutritional environment and dominate *Limnobium*.

Although competition between *Pistia* and *Salvinia* suppressed biomass yields of both species, this was not the case in the interaction between *Limnobium* and *Salvinia*. Yields of both species were hardly affected by the presence or absence of interspecific competition, except for *Limnobium* in fertilised treatments, which showed an increase in yield in response to mixing with *Salvinia*. Both species are small with leaves that do not grow high above the water surface. These similarities may explain why *Limnobium* and *Salvinia* appeared to be well matched in competitive ability. Despite appearing weak during interaction with *Pistia*, *Limnobium* was found to be slightly aggressive towards *Salvinia* in fertilised treatments. *Salvinia* growth was slightly reduced by 1:1 competition while *Limnobium* growth was enhanced, resulting in an increase in total yield compared with the yield obtained from the two species grown separately.

Relative yield calculations showed that the interaction of *Pistia* with *Salvinia*, when nutrients were in short supply, involved a greater influence of interspecific competition on yield than intraspecific competition. Both species gave higher yields when they were grown only with other individuals of the same species and so the relative yield total for the mixture was less than one. However, a more plentiful supply of nutrients removed the competitive effect, resulting in the same yield per plant per species, whether grown in a single species unit or mixed, and therefore a relative yield total close to one.

The aggressivity scores very close to zero for *Pistia* relative to *Salvinia* in both fertilised and unfertilised treatments provide further evidence of the closely matched competitive abilities of the two species. This is in contrast to the interaction between *Limnobium* and *Pistia*. It has been shown that *Pistia* is aggressive towards *Limnobium* causing its potential yield to be almost halved if the two species are grown together. The results of these two interactions suggest that *Pistia* and *Salvinia* are competitive species while *Limnobium* is less so. However, the final experiment in the series suggests that *Limnobium* can compete with *Salvinia* to which it is morphologically more similar than *Pistia*. It is not possible to

express the competitive abilities of the three species as a simple ranking because their responses varied depending on the competitor species. *Pistia* suppressed the growth of *Limnobium* while increasing its own, but when in mixture with *Salvinia* there was little effect of competition. This suggested that *Salvinia* might also be a competitive species but surprisingly its growth was slightly reduced by interaction with *Limnobium*. The effects of species interactions are therefore complex, even in simple glasshouse experiments, and can be expected to be even more complex in the communities of the Paraná floodplain where multiple species with a range of life-forms co-exist.

5.6 Conclusions

Pistia-Salvinia

- *Salvinia* responded to mixing with *Pistia* with an increase in biomass per unit canopy area in fertilised treatments. *Pistia* and *Salvinia* yields did not differ significantly between competition treatments, but yields per initial plant tended to be higher in pure culture than in 1:1 mixture.
- Total final biomass and the amount of biomass produced by each initial plant of both species were significantly greater in fertilised than unfertilised treatments. *Pistia* biomass per unit area was slightly greater in the absence of fertiliser because the increased production stimulated by the addition of fertiliser resulted in the generation of many small, new plants.
- There did not appear to be any aggressivity between the two species although the total yield of both species was greater when pure cultures were considered and not a 1:1 mixture.

Pistia-Limnobium

- There was a large size difference between the two interacting species and the small *Limnobium* plants grew much more successfully in the absence of *Pistia*. In contrast, *Pistia* benefited from mixing with *Limnobium* plants which were more benign neighbours than further *Pistia* plants.
- The provision of nutrients increased *Pistia* growth but did not affect *Limnobium*.

- *Pistia* was very aggressive towards *Limnobium* causing yield to be greatly reduced in mixed treatments compared to single-species treatments.

Salvinia-Limnobium

- Despite the low competitive ability of *Limnobium* in relation to *Pistia*, it slightly suppressed growth of *Salvinia* and benefited from mixed culture with this species.
- *Limnobium* yield per initial plant and per unit canopy area were significantly greater in the mixed treatment with the highest density of *Salvinia* while *Salvinia* did not respond significantly.
- Total biomass and percentage cover and yield per initial plant of both species increased with the addition of fertiliser. *Limnobium* biomass per final plant decreased possibly because many small new plants were produced.
- *Limnobium* was slightly aggressive towards *Salvinia*, particularly in fertilised treatments.

6 Potential use of stable isotope analysis to determine the importance of macrophytes in aquatic food webs

6.1 Aims

- To determine carbon stable isotope ratios of aquatic macrophytes which contrast in their sources of carbon dioxide or photosynthetic mechanism.
- To trace carbon derived from aquatic macrophytes into sediment underlying plant stands.
- To trace macrophyte derived carbon from the sediment into invertebrate consumers.

6.2 Introduction

It is widely accepted that aquatic macrophytes play a major role in providing habitats for other organisms (Sculthorpe 1967; Hynes 1970; Westlake 1975; Moss 1998) but any direct contribution of plant carbon to aquatic foodwebs is often considered minimal (Hutchinson 1975). The extremely high level of macrophyte production seen in tropical floodplain rivers, such as the Amazon and Orinoco, has stimulated a search for the fate of aquatic plant derived carbon. Contrasting carbon and nitrogen isotope ratios between some species of aquatic macrophytes and phytoplankton or terrestrial vegetation have allowed the use of stable isotopes as tracers of plant carbon into consumer organisms.

This approach was applied to a selection of waterbodies in the Paraná River floodplain in which it was hoped that carbon from aquatic macrophytes might be traced into primary consumer invertebrates through a detrital pathway.

The initial step in the study described in this chapter involved characterisation of $\delta^{13}\text{C}$ values of plant species employing different photosynthetic mechanisms in the floodplain of the Paraná River. One species found in the floodplain, *Paspalum repens*, is a C_4 grass known to have a $\delta^{13}\text{C}$ value of about -12‰ (Lopes 2001). This value is distinct from C_3 macrophyte and phytoplankton values and therefore provides an opportunity to follow this

enriched signal into sediments and invertebrate consumers. By sampling other species of macrophytes that use different sources of carbon, or different photosynthetic mechanisms, it was hoped to identify further species with distinct $\delta^{13}\text{C}$ which could be traced. Examples of species occurring in the study area which use different photosynthetic strategies are shown in Table 6.1.

Table 6.1 Carbon sources and photosynthetic mechanisms of some species present in the floodplain of the Paraná River.

Carbon source	Photosynthetic mechanism		
	C ₃	C ₄	SAM
Atmospheric CO ₂	<i>Eichhornia azurea</i>	<i>Paspalum repens</i>	
	<i>Eichhornia crassipes</i>		
	<i>Polygonum</i> sp.		
Dissolved CO ₂	Charophytes		<i>Potamogeton pusillus</i> <i>Egeria najas</i>
Dissolved HCO ₃ ⁻			<i>Potamogeton pusillus</i> <i>Egeria najas</i>

The potential transfer of carbon derived from the aquatic plants growing at each sub-site into the detrital foodweb was then investigated.

6.3 Methods

Sampling sites were located within a stretch of the floodplain of the Upper Paraná River, close to the city of Porto Rico. Nine different sites within the Paraná or Baía Rivers were selected in order to include sizeable macrophyte stands of the different species known to utilise contrasting carbon sources, or with contrasting photosynthetic mechanisms (Table 6.1). The sampling sites, together with the plant species sampled at each location, are listed in Table 6.2.

Table 6.2 Sampling locations, waterbody type and plant species sampled at each location.

Target species	Location	Waterbody type
<i>Eichhornia azurea</i>	Baía channel 1	Main river channel
<i>Eichhornia azurea</i>	Leopoldo backwater, Paraná	Disconnected backwater
<i>Eichhornia crassipes</i>	Lagoa das Pombas, Paraná	Connected lagoon
<i>Polygonum</i> sp.	Lagoa do Guaraná, Baía	Connected lagoon
<i>Paspalum repens</i>	Baía channel 2	Main river channel
<i>Paspalum repens</i>	Baía channel 3	Main river channel
<i>Egeria najas</i>	Pau Veio backwater, Paraná	Disconnected backwater
<i>Egeria najas</i>	Paraná channel	Main river channel
Epiphyte 1	Paraná channel	Main river channel
<i>Potamogeton pusillus</i>	Paraná channel	Main river channel
Epiphyte 2	Paraná channel	Main river channel
Charophyte	Canal Cortado, Paraná	Connected channel
Epiphyte 3	Canal Cortado, Paraná	Connected channel

At each site, three samples of live leaf tissue (entirely green), and where present three samples of dead leaf tissue (entirely brown or black), were collected from the target species. It was important to establish whether the process of senescence affected plant $\delta^{13}\text{C}$ because it is dead rather than live plant material that becomes incorporated into detritus. Up to three samples of attached algae were also collected where present. These samples were transported in plastic bags to the field station where they were rinsed in tap water. A Pedersen grab was used to collect three sediment and benthic invertebrate samples from underneath plant stands and three from the open water at the site.

Invertebrates were separated from the sediment using nested sieves, rinsed in tap water, sorted and identified. Macrophyte-associated invertebrates were sampled by collecting 1 m² of plant material, transporting this back to the field station and then manually removing macroinvertebrates on a catch per unit effort basis (30 minutes per sample). Animals were rinsed in tap water and sorted and identified. Plant, sediment and animal samples were oven dried at 60°C. The algae and vascular plant samples were prepared for stable isotope analysis by freezing with liquid nitrogen and milling. Sediment samples were ground to a fine powder by hand and then hydrochloric acid was added to a sub-sample to test for the presence of carbonates which would confound the analysis.

Approximately 0.7 mg of powdered macrophyte sample was loaded into a 5 mm x 8 mm tin capsule and combusted in a Carlo Erba C/N/S analyser interfaced with Finnigan Tracer Matt continuous flow isotope ratio mass spectrometer. The samples were oxidised over hot furnaces in an oxygen-rich helium carrier gas flow. All oxidation products (e.g., water,

sulphur dioxide) except carbon dioxide and nitrogen were chemically stripped from the sample combustion products prior to chromatographic separation of nitrogen from carbon dioxide and introduction of each gas to the mass spectrometer for measurement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Repeat analysis of international and internal laboratory standards shows that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can usually be measured with precision and accuracy of $\leq \pm 0.2\text{‰}$. For analyses of sediment, the size of tin capsule and weight of samples was adjusted (6-20mg of sediment was required) to provide approximately 0.4mg of carbon. The nitrogen concentration was too low to allow measurement of $\delta^{15}\text{N}$. Analysis was conducted at the Life Sciences Community Stable Isotope Facility, Scottish Universities Environmental Research Centre, East Kilbride, UK with the help of Dr Susan Waldron who operated the mass spectrometer, collected the results of the analysis and, together with Dr Matthew O'Hare (University of Glasgow), helped with their interpretation.

Live plant tissue $\delta^{13}\text{C}$ was compared with dead, and open water sediment $\delta^{13}\text{C}$ compared with sediment collected underneath plant stands within individual sites using t-tests. Analyses were carried out using Minitab 13.

6.3.1 Calculating the relative importance of two carbon sources

A two end-member mixing model can be used to calculate the relative contributions of two different sources of carbon with distinct $\delta^{13}\text{C}$ values to a sediment carbon pool (Vitarello *et al.* 1989), or to the diet of an animal (Forsberg *et al.* 1993). This requires the two principal carbon sources to be identified. In the main channel of the Paraná River, because the current velocity is so rapid and the water is relatively low in organic nitrogen and phosphorus sources, few macrophytes other than the streamlined rooted, submerged species can grow. The other source of carbon within the channel is the phytoplankton community, although this is a limited source in the main channel of the Paraná River compared with floodplain waterbodies (Thomaz, Roberto & Bini 1997). Otherwise, carbon must enter the river from upstream (as predicted by the River Continuum Concept; Vannote *et al.* 1980), or from floodplain (as predicted by the Flood Pulse Concept; Junk, Bayley & Sparks 1989) or terrestrial sources. C_4 macrophytes are not common in the floodplain and the vegetation is strongly dominated by the C_3 species, *Eichhornia azurea*, which obtains carbon from the atmosphere. The principal potential carbon sources are therefore phytoplankton (-31.7‰), terrestrial riparian vegetation (-30.1‰), C_3 macrophytes (-28.4‰) (average values calculated for the study locality by Lopes 2001) and submerged plants and algae ($\delta^{13}\text{C}$ determined during the study). The percentage contribution of

submerged plants and attached algae to the sediment carbon pool at the Paraná channel site can be calculated using the following equations. The maximum and minimum potential contributions of submerged plant and attached algae carbon can be calculated by inserting into the equation in turn the most depleted (phytoplankton; Equation 6.1) and least depleted (C_3 macrophytes; Equation 6.2) alternative carbon sources at the site (c.f. Forsberg *et al.* 1993).

Equation 6.1

$$\% C_{\text{submerged}} = [1 - (\delta^{13}C_{\text{sediment}} - \delta^{13}C_{\text{submerged}}) / (\delta^{13}C_{\text{phytoplankton}} - \delta^{13}C_{\text{submerged}})] \times 100$$

Equation 6.2

$$\% C_{\text{submerged}} = [1 - (\delta^{13}C_{\text{sediment}} - \delta^{13}C_{\text{submerged}}) / (\delta^{13}C_{\text{macrophytes}} - \delta^{13}C_{\text{submerged}})] \times 100$$

$\% C_{\text{submerged}}$ = percentage of carbon contributed by submerged plants and attached algae

$\delta^{13}C_{\text{sediment}}$ = average $\delta^{13}C$ value for sediment samples collected underneath submerged plants and attached algae

$\delta^{13}C_{\text{submerged}}$ = average $\delta^{13}C$ value of submerged plant and attached algae samples

$\delta^{13}C_{\text{macrophytes}}$ = average $\delta^{13}C$ value of C_3 macrophytes

$\delta^{13}C_{\text{phytoplankton}}$ = average $\delta^{13}C$ value for phytoplankton in the Paraná River

6.4 Results

6.4.1 Plant Carbon

Table 6.3 shows mean $\delta^{13}C$ values of samples of live and dead leaf tissue collected from a selection of aquatic macrophytes that are common in the study area. The study aimed to examine within-site carbon transfer processes and so sites were chosen in order to sample this range of species expected to have contrasting $\delta^{13}C$. In most cases therefore, samples differed in both species and collection site and so it was not possible to make meaningful comparisons of $\delta^{13}C$ between species.

However, when groups of samples sorted by photosynthetic strategy were compared, distinct ranges in $\delta^{13}\text{C}$ were observed (Table 6.4). The C_3 species with aerial leaves were most ^{13}C depleted with only a small range in $\delta^{13}\text{C}$ between species. The charophyte samples (collected at only one site) were slightly more enriched, followed by the submerged species which utilise bicarbonate ions during photosynthesis. The C_4 *P. repens* samples were the most ^{13}C enriched. $\delta^{13}\text{C}$ of *P. repens* differed between the two sites from which it was collected, although in both cases it was distinct from $\delta^{13}\text{C}$ of the other photosynthetic groups. $\delta^{13}\text{C}$ of the epiphyte samples, collected from three different host species at two different sites, fell within the range of submerged bicarbonate-using macrophytes.

Table 6.3 Mean $\delta^{13}\text{C}$ (standard deviation in brackets) of live and dead plant tissue.

Target species	Location	$\delta^{13}\text{C}$ live (‰)	n	$\delta^{13}\text{C}$ dead (‰)	n
<i>Eichhornia azurea</i>	Baía channel 1	-27.1 (0.2)	3	-27.5 (0.6)	3
<i>Eichhornia azurea</i>	Leopoldo backwater	-27.9 (0.4)	3	-28.9 (0.3)	3
<i>Eichhornia crassipes</i>	Lagoa das Pombas	-26.9 (0.7)	3	-26.7 (0.7)	3
<i>Polygonum</i> sp.	Lagoa do Guaraná	-28.0 (0.5)	3	-28.0 (0.1)	3
<i>Paspalum repens</i>	Baía channel 2	-14.1 (0.5)	3	-13.8 (0.4)	3
<i>Paspalum repens</i>	Baía channel 3	-11.8 (0)	3	-12.9 (0.3)	3
<i>Egeria najas</i>	Pau Veio backwater	-20.4 (0.5)	3		
<i>Egeria najas</i>	Paraná channel	-20.1 (0.4)	2		
<i>Potamogeton pusillus</i>	Paraná channel	-17.0 (0.2)	3		
Charophyte	Canal Cortado	-24.1 (0.6)	3		
Epiphyte 1 (<i>E. najas</i>)	Paraná channel	-20.4 (2.2)	3		
Epiphyte 2 (<i>P. pusillus</i>)	Paraná channel	-19.2 (0.6)	3		
Epiphyte 3 (Charophyte)	Canal Cortado	-18.7	1		

The $\delta^{13}\text{C}$ values of the emergent and floating C_3 and C_4 macrophytes and submerged bicarbonate-using macrophytes were similar to other measurements that have been made in the floodplain (-28.7 to -28.9‰ for aerial-leaved C_3 , -13.0‰ for C_4 , -19.7‰ for *Egeria* sp.; Lopes 2001). Table 6.4 shows the distinct ranges in $\delta^{13}\text{C}$ seen when plant species were classified according to photosynthetic strategy.

Table 6.4 Range of $\delta^{13}\text{C}$ values observed in relation to photosynthetic strategy of aquatic macrophyte species.

Species	Photosynthetic strategy	Range of $\delta^{13}\text{C}$
<i>Paspalum repens</i>	Emergent C_4	-11.8 to -14.6
<i>Potamogeton pusillus</i>	Submerged HCO_3^- user	-16.8 to -21.0
<i>Egeria najas</i>		
Charophyte	Submerged C_3 CO_2 user	-23.7 to -24.8
<i>Eichhornia azurea</i>	Emergent C_3	-26.0 to -28.5
<i>Eichhornia crassipes</i>		
<i>Polygonum</i> sp.		

Mean $\delta^{13}\text{C}$ values differed by a maximum of 1.1‰ between live and dead plant material collected for the floating and emergent species (Table 6.3). Values were statistically significantly different for *E. azurea* at Leopoldo backwater (t-test $p=0.043$) and for *P. repens* at Baía channel 3 (t-test $p = 0.032$). However, the size of change in $\delta^{13}\text{C}$ between live and dead tissue was so small that this would be unlikely to interfere with tracing plant carbon. $\delta^{13}\text{C}$ of plant material therefore does not appear to alter greatly during senescence and so it was considered valid to look for the influence of $\delta^{13}\text{C}$ values of live plants in sediment underneath plant stands.

6.4.2 Plant Nitrogen

Table 6.5 Mean $\delta^{15}\text{N}$ of live and dead plant tissue (standard deviation in brackets).

Target species	Location	$\delta^{15}\text{N}$ live (‰)	n	$\delta^{15}\text{N}$ dead (‰)	n
<i>Eichhornia azurea</i>	Baía channel 1	4.8	2	3.4	3
<i>Eichhornia azurea</i>	Leopoldo backwater	2.5 (1.1)	3	5.7 (0.4)	3
<i>Eichhornia crassipes</i>	Lagoa das Pombas	9.3 (0.9)	3	9.7	2
<i>Polygonum</i> sp.	Lagoa do Guaraná	5.9	2	3.23 (2.1)	3
<i>Paspalum repens</i>	Baía channel 2	-0.2	2	1	3
<i>Paspalum repens</i>	Baía channel 3	2.3 (0.3)	3	2.2 (0.6)	3
<i>Egeria najas</i>	Pau Veio backwater	8.1 (0.7)	3		
<i>Egeria najas</i>	Paraná channel	5.9 (0.7)	3		
<i>Potamogeton pusillus</i>	Paraná channel	10.0 (0.7)	3		
Charophyte	Canal Cortado	10.5 (1.6)	3		
Epiphyte 1	Paraná channel	8.1 (0.4)	3		
Epiphyte 2	Paraná channel	8.5 (0.6)	3		

Mean $\delta^{15}\text{N}$ values for live and dead plant material were very variable between samples and in most cases were much higher than the mean values of 0.4 to 4.7‰ (depending on growth form) given by Lopes (2001) but within the range of measurements of individual samples (Table 6.5). In the three species sampled at two sites, *E. azurea*, *P. repens* and *P. pusillus*, $\delta^{15}\text{N}$ differed substantially between sites. In some samples there were large differences in $\delta^{15}\text{N}$ between live and dead tissue but this was also not consistent within species. For example, dead *E. azurea* leaves were less ^{15}N enriched than live leaves at Baía 1 while the opposite was true at Leopoldo backwater. Live and dead leaf samples of *E. crassipes* collected from Lagoa das Pombas had similar $\delta^{15}\text{N}$. This was also the case for *P. repens* collected from Baía 3. Although the data set was incomplete and replicate samples of the same species from different sites were not available, the $\delta^{15}\text{N}$ values suggest a possible contrast in ^{15}N enrichment between submerged and emergent plants. Submerged plant $\delta^{15}\text{N}$ was significantly higher than emergent plant $\delta^{15}\text{N}$ (t-test, $p = 0.001$).

6.4.3 Sediment

Table 6.6 Mean $\delta^{13}\text{C}$ of sediment samples (standard deviation in brackets) collected from underneath plant stands or from adjacent open water.

Site	Species	$\delta^{13}\text{C}$ under	n	$\delta^{13}\text{C}$ open	n
Paraná channel	<i>Egeria najas</i>	-23.3 (0.2)	3	-22.9 (0.3)	3
Paraná channel	<i>Potamogeton pusillus</i>	-22.9 (0.3)	3	-22.9 (0.3)	3
Canal Cortado	Charophyte	-24.9 (0.6)	3	-25.0 (0.5)	3
Lagoa das Pombas	<i>Eichhornia crassipes</i>	-25.6	2	-24.4 (1.7)	3
Baía channel 3	<i>Paspalum repens</i>	-27.8	2	-26.4 (0.6)	3
Pau Veio backwater	<i>Egeria najas</i>	-25.5 (0.3)	3	-25.4 (0.9)	3

$\delta^{13}\text{C}$ of sediment samples collected underneath plant stands was similar at all sites to $\delta^{13}\text{C}$ of sediment collected in the same area but in open water (Table 6.6). This suggests that plant detritus did not accumulate to a great extent underneath the plant stands but was soon mixed with other carbon inputs resulting in a similar sediment isotopic composition throughout the site. At the Paraná channel site, $\delta^{13}\text{C}$ of sediment collected from underneath *E. najas* was significantly higher than sediment collected in the open water (t-test $p=0.047$) but the mean values were quite similar suggesting that carbon inputs were not very different between the two locations.

The ^{13}C enriched isotope signature of *P. repens* was not reflected in its underlying sediment which had a much less enriched $\delta^{13}\text{C}$ value (Table 6.6). $\delta^{13}\text{C}$ of sediment collected from underneath *E. crassipes* and the charophytes was similar to the values found for the plant tissue, which were also within the range of values associated with terrestrial C_3 vegetation. The sediment underneath *E. najas* and *P. pusillus* was less enriched in $\delta^{13}\text{C}$ than the plant tissue but much more enriched than potential terrestrial or phytoplankton carbon sources.

The lack of a direct relationship between plant $\delta^{13}\text{C}$ and $\delta^{13}\text{C}$ of the underlying sediment created a problem in the initial study design which had relied on the assumption that it would be possible to trace plant carbon first into the sediment before potential consumption by invertebrates. With similar sediment $\delta^{13}\text{C}$ both underneath and outwith plant stands, at most sites it was not possible to show that a particular aquatic plant species was the main source of carbon contributing to the underlying sediment. This in turn created a problem in trying to use carbon isotope ratios to link the collected invertebrates to these plants through the sediment and so invertebrate samples were not analysed.

6.4.4 Carbon contribution from submerged plants

At the Paraná channel site, the enriched $\delta^{13}\text{C}$ of the sediment did suggest that the submerged macrophytes and their epiphytes growing there could be contributing a significant amount of carbon to it. The mean $\delta^{13}\text{C}$ value for submerged species (*E. najas*, *P. pusillus* and attached epiphytes) at the Paraná channel site was calculated as -19.2‰ ($n=11$). $\delta^{13}\text{C}$ values are not available for all possible sources of carbon in the river, but the most depleted alternative carbon source with known $\delta^{13}\text{C}$ is phytoplankton ($\delta^{13}\text{C} = -32.4\text{‰}$; Lopes 2001). Mean sediment $\delta^{13}\text{C}$ calculated from samples collected under *E. najas* and *P. pusillus* and in the open water was -23.1‰ ($n=9$).

By taking these average values and assuming that phytoplankton was the most $\delta^{13}\text{C}$ depleted carbon input to the sediment pool, an estimated maximum contribution of submerged plant and epiphyte carbon to the sediment at this site was calculated as 70%.

By replacing the phytoplankton $\delta^{13}\text{C}$ value in the mixing model with the value for the most enriched likely carbon input, C_3 macrophytes (-28.4‰), a minimum contribution by submerged macrophytes of 58% was calculated.

6.5 Discussion

Four distinct $\delta^{13}\text{C}$ ranges were measured in four groups of aquatic macrophytes each using a different carbon source or photosynthetic mechanism. These ranges could be understood in light of the $\delta^{13}\text{C}$ values associated with each of the carbon sources and photosynthetic processes. The relatively ^{13}C enriched submerged species provided an opportunity to look for macrophyte carbon in the underlying sediment. The enriched sediment $\delta^{13}\text{C}$ value suggested that macrophyte carbon was entering the detritus pool at this site. A mass-balance equation (making substantial assumptions) suggested a maximum contribution of 70%. The plant $\delta^{13}\text{C}$ values agree with those of a larger scale study continuing on the Paraná floodplain (Lopes 2001).

The plant nitrogen data were initially obtained to help to assign trophic levels to consumers. Although this was no longer required, the results were useful in confirming the high spatial variability in $\delta^{15}\text{N}$ of macrophytes in the Paraná floodplain and indicating that large numbers of very local samples would be necessary to make use of $\delta^{15}\text{N}$ for estimating trophic levels in a food web study. The $\delta^{15}\text{N}$ data for live plant tissue may be reflecting spatial variation in nitrogen resources, or alternatively contrasting nitrogen uptake and assimilation mechanisms between submerged and emergent species.

Stable isotope techniques provide a tool for tracing carbon flow but the existence of carbon sources with highly distinct isotopic compositions is vital. Furthermore, knowledge of physical processes affecting the distribution of carbon sources in relation to potential consumers, and the ability of consumers to feed selectively upon them, can increase the power of stable isotope methods vastly. It was hoped initially that it would be relatively easy to detect carbon fixed by the C_4 grass, *P. repens* because it is particularly enriched in ^{13}C . However, underneath this species the carbon isotopes in the sediment did not reflect plant carbon. In this study, the random selection of sites may not have been the best approach because this meant that *P. repens* was only collected from lotic habitats where senescent material was less likely to accumulate. This was the most common type of habitat in which *P. repens* was observed, but this species can grow in lentic or semi-lentic environments too. A further step in site selection could be to locate waterbodies where the species of interest is highly dominant so that other sources of carbon would be less likely to disguise any evidence of invertebrates consuming the macrophyte. However, such strict criteria for site choice could result in perhaps unusual habitats being studied which may not

provide a representative impression of the functioning of food webs in the Paraná floodplain.

6.6 Conclusions

- Four distinct $\delta^{13}\text{C}$ ranges were measured in four groups of aquatic macrophytes reflecting differences in carbon source or photosynthetic mechanism.
- The submerged species sampled were relatively enriched in ^{13}C providing an opportunity to look for evidence of macrophyte carbon in the underlying sediment.
- The underlying sediment was enriched in ^{13}C suggesting that macrophyte carbon was entering the detritus pool.
- A mass balance equation (making substantial assumptions) suggested that macrophytes had contributed a maximum of 58-70% of the carbon in the sediment.
- The similarity of sediment carbon isotope signatures underneath and outwith plant stands at most sites prevented the investigation of whether invertebrates were consuming macrophyte carbon.
- The plant nitrogen data confirmed high spatial variability of $\delta^{15}\text{N}$ in the macrophytes of the Paraná floodplain. This may reflect spatial variation in nitrogen sources or contrasting uptake and assimilation mechanisms between submerged and emergent species.
- Intensive sampling would be required to use $\delta^{15}\text{N}$ values for estimating trophic levels in a food web study on the Paraná River.

7 Discussion

The aim of this project was to describe the vegetation of a stretch of the Paraná River floodplain and to investigate which natural or human-imposed factors might be controlling its characteristics, its capacity for biodiversity support and its potential to provide an economic resource.

7.1 Summary of results

7.1.1 *Current status of the floodplain vegetation*

The current status of the vegetation of three floodplain zones (aquatic habitats, bank and shore habitats and adjacent floodplain areas) was described using data collected during surveys of plant communities and their physical attributes at a range of sites, varying in location, topography and waterbody type. Analysis of these data showed that at least three distinct aquatic vegetation communities existed in the study area. Two communities were found in the bank and shore zone and two in the floodplain zone. These were more loosely defined than the aquatic communities due to lower taxonomic resolution during identification of terrestrial species. During the field surveys, a number of environmental variables were measured at the sampling sites and the level of livestock grazing was assessed. Comparison of these variables between plant community types showed that the communities were associated with contrasting environmental characteristics.

In the aquatic zone, one community type (*Eichhornia azurea* and various free-floating species) was linked with deep, semi-lotic or lotic water with low electrical conductivity and sediment that was rich in nitrogen and phosphorus. The second type was linked with shallow, lentic water with high electrical conductivity and sediment rich in nitrogen and phosphorus (*E. azurea* strongly dominant), and the third was linked with fast-flowing, very clear water and very low levels of nitrogen and phosphorus in the sediment (submerged species).

In the bank and shore zone, two contrasting vegetation types were found, one associated with gently sloping, low elevation banks where the soil tended to be more nutrient-rich (*Polygonum-Ludwigia*), and the other with steeper, higher elevation banks where the soil was poorer (*Poaceae*). Sub-groups of these main communities were also suggested.

Two different broad vegetation types were also found in the adjacent floodplain vegetation. The dominant vegetation type was indicated by grasses and creepers and was associated with low soil nitrogen and calcium. A small number of sites supported a community in which *Polygonum* species were more important. This community was associated with higher soil nitrogen and calcium. Analysis of the species data suggested that there might be a number of grass-dominated sub-communities but the problem of identifying grasses that were not in flower made it difficult to define further communities.

The type of vegetation community is thus influenced by the specific combination of environmental conditions at each site. Activities in the floodplain that might alter environmental conditions, for example, water velocity or depth in aquatic environments or soil nutrient levels in terrestrial environments, can therefore be expected to interfere with the distribution and abundance of these vegetation communities.

The communities also differed in collective vegetation characteristics, suggesting that they might provide different types of habitats for other organisms. Terrestrial herbivores may have preferences for particular food plants associated with different communities.

Contrasting growth forms between aquatic plant communities can be expected to result in variation in their suitability for providing shelter for fish and invertebrates, oviposition sites, and attachment surfaces for epiphytes and other organisms which provide a food source. The aquatic plant community comprised mainly of surface floating species, such as *Salvinia* sp., *Eichhornia crassipes* and *Limnobium laevigatum*, provides a habitat for terrestrial insects as well as possibly providing shelter for fish in its submerged roots.

Changes in the type or quantity of different plant communities can therefore be expected to have implications for the other organisms that they support.

7.1.2 Factors influencing vegetation patterns

Factors regulating the floodplain vegetation were further investigated by describing the responses of species and of collective vegetation structure to environmental gradients.

When the 2000-2001 aquatic data set was considered, species assemblages were found to respond most strongly to gradients in the amount of light available at the bottom of the waterbody, water depth, sediment nitrogen and sediment phosphorus. Submerged species tended to be associated with low sediment nitrogen and phosphorus and low water phosphorus, while *E. azurea* was most successful in conditions of high sediment nitrogen, phosphorus, calcium and iron and water phosphorus. Species richness tended to increase

with water depth and decrease with sediment calcium; biomass decreased with the amount of light available at the sediment and responded quadratically to water nitrogen; and canopy height decreased with water conductivity.

At bank and shore sites, a number of relationships were found during analysis of the individual and combined data sets. Species richness decreased with soil nitrogen, phosphorus, calcium and pH and the distance of the sampling site from the associated waterbody. Biomass was related to soil iron and phosphorus, canopy cover was related to soil calcium and elevation and stem density was related to elevation and distance from the waterbody.

In the adjacent floodplain zone, species richness tended to decrease with soil nitrogen; canopy height increased with soil phosphorus; biomass responded quadratically to soil phosphorus; and stem density increased with distance from the waterbody, decreased with soil phosphorus and responded quadratically to soil pH and calcium.

Aquatic vegetation and environment survey data collected between 1999 and 2001 were also used to make a more detailed analysis of the dominant aquatic species in the floodplain, *Eichhornia azurea*, and of *E. crassipes* which was less abundant but was also observed at a large number of sites. Because these species occurred so frequently in a wide range of environmental conditions and as part of different vegetation communities (particularly *E. azurea*), the effect of environmental gradients and community composition on their success was studied by analysis of their morphological traits. Total leaf dry weight, leaf thickness and the ratio of leaf weight to root weight of *E. azurea* differed significantly between the different vegetation communities of which it was a component. *E. azurea* tended to be most successful when interacting with other species with aerial leaves but lost some of its competitive advantage in habitats where environmental conditions favoured submerged species. *E. crassipes* was a component of two vegetation communities and differed in total leaf weight, total leaf area and total plant weight between the communities. *E. azurea* and *E. crassipes* appeared to replace each other in the vegetation community according to whether the bank-rooted or free-floating form was most suitable for a particular site. Analysis of the response of *E. azurea* to environmental gradients showed that plants tended to be larger overall in deeper water habitats with higher water clarity. *E. crassipes* also tended to increase in size with water depth but decreased with sediment phosphorus and responded quadratically to sediment calcium and to light availability at the sediment.

7.1.3 Implications for floodplain management

The information obtained about the association of particular vegetation types with particular environmental conditions and the relationships of species and vegetation structure with environmental gradients may be useful for making management decisions about the floodplain. In management for biodiversity, if the vegetation type important in supporting an organism of interest is identified then the environmental conditions associated with this vegetation type can be targeted for careful monitoring. Similarly, if a particular vegetation type is of economic value, perhaps because it provides a habitat for desirable fish species then the environmental factors to which this vegetation type is sensitive can be monitored to ensure that it is sustained. Furthermore, the responses of species to specific environmental gradients and the predictive relationships found between vegetation structure and environmental variables may be used to predict the outcome of a change in land use in the floodplain.

7.1.4 Development of project themes

The analysis of the survey data collected from the floodplain produced an extensive amount of information about the types of vegetation growing in the floodplain and how these might be influenced by environmental factors that may vary naturally or as a result of human activities. During consideration of the aims of the project, three aspects of the functioning of the floodplain vegetation were selected for study in greater detail. These were the impact of livestock grazing on terrestrial vegetation, aquatic plant competition (particularly in the context of potential future changes in the nutrient status of floodplain waterbodies) and the role of aquatic macrophytes as primary producers in aquatic foodwebs in the floodplain.

Impacts of livestock grazing

Grazing was an important topic because it was the most conspicuous factor contributing to degradation of terrestrial vegetation on the islands in the Paraná channel and in some other parts of the floodplain. A large proportion of Paraná state was deforested in the past to make land available for arable farming but many areas were subsequently turned over to cattle grazing. Although the study area is now protected by legislation and most cattle have been removed, some remain and continue to prevent regeneration of vegetation. Management of grazing practices in the floodplain must be a major aspect of protecting floristic diversity and maintaining the capacity of the vegetation to support other

organisms. The Brazilian environment agencies are currently working to encourage vegetation regeneration on the islands of the Paraná River. The detailed study of short-term vegetation recovery on Ilha Mutum therefore provides useful information on the initial response of previously grazed vegetation to the removal of this pressure. The experiment involving application of a disturbance treatment to an ungrazed wet grassland provides a starting point for understanding how much grazing pressure natural floodplain vegetation might be able to withstand without being seriously degraded.

Protection of formerly grazed vegetation from cattle, using exclosures, resulted in rapid regrowth of vegetation at two locations on Mutum Island. In the first experiment, which was positioned in a dry area of the island, species richness increased in response to removal of the grazing pressure. In the second experiment, which was positioned in a wetter part of the island, this was not the case but an additional response was seen of reduced bare ground in plots protected from grazing. The differences in responses may be explained by the wetter area being more susceptible to trampling damage and more limited in the number of species adapted to occasional flooding of this site by the adjacent lagoon. In general, the exclosure experiments showed that the island vegetation had the capacity for rapid initial regeneration of biomass and canopy height and possibly an increase in species richness following removal of grazing pressure. In one experiment, protection from grazing also caused a decrease in bare ground and, in another, an increase in the contribution of graminoid species biomass to total biomass. This increase in graminoids suggests an increase in the palatability of the vegetation to livestock (Quintana, Monge & Malvárez 1998). The cutting experiment showed that natural wet grassland vegetation recovered quickly from a single disturbance and this work could be extended to investigate further the possibility of finding a sustainable level of grazing in the floodplain.

Competition in free-floating plant communities

Patterns in plant species distributions and abundances are influenced by the interaction of environmental and biotic factors and so are sensitive to changes in the relative importance of these factors. Competitive interactions between aquatic plant species in the Paraná floodplain were chosen for study because these can be expected to vary in importance in controlling floodplain vegetation communities due to alteration in the balance of stress and disturbance which can be expected to result from increased river flow regulation.

Competition experiments were designed to examine the interactions of pairs of floating aquatic plant species that are common in the Paraná floodplain. The experimental

conditions were clearly highly artificial but allowed the pairwise interactions between the three study species, *Pistia stratiotes*, *Salvinia auriculata* and *Limnobium laevigatum*, to be studied in detail. The experiments were carried out in both low and high nutrient water so that the results could be used to suggest the possible effects of alteration in the nutrient status of floodplain waterbodies on competitive interactions between floating aquatic plants.

The experiments showed that interaction between *Pistia* and *Salvinia* slightly suppressed the yield of both species in low nutrient conditions but not in high nutrient conditions. Both species seemed to have similar competitive ability. *Pistia* responded to higher nutrient conditions with increased propagule production. The interaction of *Pistia* and *Limnobium* caused an increase in *Pistia* yield and a decrease in *Limnobium* yield and an overall increase in total yield. *Pistia* yield also increased in response to increased water nutrients but *Limnobium* did not respond. *Limnobium* appeared to have very low competitive ability in relation to *Pistia*. However, *Limnobium* yield was not suppressed by interaction with *Salvinia*, suggesting that the relative competitive ability of the three study species was more complicated than a simple ranking.

The implications of the results for the Paraná floodplain, where water fertility may be declining, could be reduced yield from individuals of *Salvinia* and *Pistia* (and also *Limnobium* in some communities), changes in population physical structure and reduced propagule generation. Biomass per unit area of *Pistia* coverage could be expected to increase due to reduced vegetative reproduction. Biomass per unit area of *Salvinia* could be expected to decline, especially in the presence of *Pistia*. Reduced coverage of *Salvinia* can also be considered a reduction in propagule generation. The capacity of an individual plant to reproduce vegetatively depends on the number of viable sections into which it can divide, which in turn may be a function of the length and degree of branching of the plant. The results of the *Pistia*-*Salvinia* experiment suggest that nutrient stress would result in mutual suppression of growth of the two species in situations where they co-exist. However, their relative success would not be affected as their competitive abilities are well matched.

The results suggest that reduced nutrient availability in floodplain environments could cause a decline in *Pistia* reproduction and favour growth of individuals. This could give the weaker competitors, such as *Limnobium*, a better chance to establish populations. The opposite effect of nutrient enrichment could be expected to cause the ousting of species, such as *Limnobium*, from a waterbody colonised by *Pistia*. Although *Pistia* tended to be

observed at low density in the study area, very large populations develop in other parts of the Paraná River, such as the Itaipu Reservoir (FUEM/NUPELIA-Itaipu Binacional 1997).

The lack of aggressivity between *Pistia* and *Salvinia* explains the co-existence of these two species in natural conditions. During the floodplain surveys, *Salvinia* sp. was the dominant component of floating communities and so was also present when *Pistia* was present, although *Pistia* tended to occur at low abundance. However, the poor performance of *Limnobium* relative to *Pistia* suggests that these two species are unlikely to simultaneously maximise their growth if occurring in the same place. These two species could be expected to co-exist at low density in relatively uncrowded waterbodies where disturbance may be an additional factor regulating community composition. The results of the aquatic vegetation surveys supported this theory as *Pistia* and *Limnobium* were not observed at high densities but tended to co-occur, both at very low density.

Although *Limnobium* was clearly lacking in adaptations to allow it to compete with *Pistia*, this was not the case when its interaction with *Salvinia* was considered. The outcome of the interactions was specific to each pair of species. The experiments with *Pistia* suggested that *Salvinia* had high competitive ability and *Limnobium* had low competitive ability. However, when these two species were grown together, it was *Limnobium* that was found to be slightly aggressive toward *Salvinia*. Where environmental conditions were appropriate, *Salvinia* and *Limnobium* could therefore be expected to grow together in the same community. This agrees with the distribution of these species observed during vegetation surveys, as *Salvinia* sp. was usually abundant at sites where *Limnobium* grew.

The plant competition experiments suggested some effects of a biotic factor acting on aquatic vegetation patterns in the floodplain. In order to understand as much as possible about how the floodplain vegetation functions, it is important to consider interactions between organisms as well as environmental gradients and human impacts.

Role of macrophytes in aquatic foodwebs

The biodiversity support role of floodplain vegetation may include provision of food, shelter from prey and suitable habitats for reproduction for animals, or the creation of suitable microclimates or growth sites to support an increased diversity of plant life. Primary production of aquatic macrophytes in tropical floodplains is so high that it might be presumed that food provision is a major function of this vegetation. For this reason, the

importance of aquatic macrophytes in aquatic foodwebs was the third topic to be investigated in detail.

At one site, evidence obtained suggested that submerged aquatic plants were contributing a substantial amount of carbon to the detrital carbon pool in the sediment underlying macrophyte stands. However, at the remaining sites, even where the macrophyte species were found to have distinctive carbon isotope signatures, macrophyte derived carbon was not detectable underneath plant stands and the sediment carbon pool was isotopically similar to samples taken from outwith plant stands. It is likely that carbon derived from other sources was mixing with macrophyte derived carbon at these sites. The similarity in carbon isotope signatures between sediment underneath plant stands and sediment under open water prevented plant carbon from being traced into potential consumer invertebrates.

Although it was not possible to trace plant carbon into primary consumers, this study produced information about the carbon and nitrogen isotope signatures of different aquatic plant species growing in different areas of the Paraná floodplain. As isotope signatures can vary spatially and temporally, this information may be useful in future foodweb studies carried out within the floodplain. The data obtained were also used to suggest relationships between carbon isotope signatures and the range of photosynthetic strategies employed by different macrophyte species.

7.2 Discussion of results

7.2.1 Vegetation across the floodplain habitats

Campos and Souza (1997) outline the general vegetation types found in the floodplain of the last undammed stretch of the Paraná River in Brazil. Originally, two types of semi-deciduous seasonal forest grew in the region; semi-deciduous seasonal alluvial forest and semi-deciduous seasonal sub-montane forest. The sub-montane forest formerly occupied rounded hilltops and gentle slopes, and some component species still survive near Porto Rico, but this forest type is now considered virtually extinct in the region. The alluvial forest still persists, although often modified, on the alluvial plains, on some islands and on stream banks. This forest type is separated into two sub-types, one associated with frequently flooded soils and so including flood-tolerant species, and the other associated with drier soils. Other vegetation types include pioneer communities, which develop in areas influenced by rising and falling river levels. Soil and hydrological conditions are therefore very variable and vegetation patches may expand and contract according to the

prevailing environmental conditions. More permanently wet areas support aquatic macrophyte communities, while higher areas that are less frequently flooded tend to support grass communities.

Information on the species present in the floodplain and on the communities that they form has come from on-going surveys conducted by researchers at NUPELIA as well as from vegetation studies carried out when plans were proposed for hydroelectric schemes downstream of the study area at Ilha Grande (subsequently abandoned) and upstream at Porto Primavera (now in place). Most research at NUPELIA has focused on the forest vegetation and the aquatic vegetation. The remnants of riparian forest have been surveyed and analysed phytosociologically. Wetland vegetation and non-forest floodplain vegetation in general have received less attention. Studies on aquatic vegetation have included investigation of biomass responses of different species to water level variation (Bini 1996) and estimation of species diversity (Bini, Thomaz & Souza 2001; Souza, Thomaz & Bini 2002), as well as investigation of the effects of aquatic plant decomposition on water quality (Pagioro & Thomaz 1999). In 1999, Murphy *et al.* (2003) conducted an extensive survey of vegetation and environmental variables in a variety of floodplain waterbodies (single samplings of 45 stations within a period of six weeks) and used this information to identify aquatic vegetation communities; to relate variations in species assemblage and characteristics of the dominant species to environmental gradients; and to form predictive equations of species richness and community biomass from environmental variables and dominant species traits. The first two results chapters of this thesis built on the results of the 1999 surveys to include sampling over three consecutive years and to encompass the vegetation of the banks of the floodplain waterbodies and adjacent floodplain areas.

The aquatic environment

Environmental comparisons

Measurements of water and sediment chemistry and light attenuation in the water column were generally in agreement with those reported by Murphy *et al.* (2003) from their survey conducted in 1999 and within the ranges recorded during several other studies in the floodplain waterbodies (Thomaz, Roberto & Bini 1997). Water depth, light attenuation, the proportion of the water column sufficiently illuminated for plant growth, water pH, water total Kjeldahl nitrogen and total phosphorus and sediment total Kjeldahl nitrogen, total calcium and total iron were mainly distributed around the mean values reported by

Murphy *et al.* (2003). However, the electrical conductivity of the water was generally lower, while sediment ADAS extractable phosphorus was generally higher. Sediment redox potential also differed between years. Sediment conditions were particularly reducing in 1999 (Murphy *et al.* 2003), indicating anoxic conditions, the absence of nitrate and the presence of manganous and ferrous ions (Laanbroek 1990). In 2000, redox potential suggested less reducing conditions and a much less hostile environment for plant growth with greater availability of oxygen and nitrogen and lower levels of potentially toxic ions. Measurements of redox potential in 2001 suggested conditions intermediate between these two states.

Aquatic macrophyte communities

Due to the complexity of the aquatic habitats in the floodplain and the size of the area, the process of compiling a comprehensive species list is on-going. To date, a total of 62 species of aquatic macrophytes have been recorded in the Upper Paraná River floodplain (Thomaz *et al.* 2004). Fifty aquatic species were recorded by Bini, Thomaz & Souza (2001) during intensive surveys of multiple floodplain waterbodies carried out in the low water period of the flood cycle. Fewer species were encountered by Murphy *et al.* (2003) (28 species) and during the surveys conducted for this thesis (at least 31 species) because the sampling designs were less intensive and involved recording several vegetation and environment factors in addition to the species list. In the survey conducted in 1999 by Murphy *et al.* (2003), and in the surveys conducted for this thesis in 2000, 2001 and 2002, *Eichhornia azurea* was by far the most common species encountered. When only lagoons connected to the Paraná, Baía or Ivinheima Rivers were considered by Bini, Thomaz & Souza (2001), *Polygonum ferrugineum* was the most frequently observed species and *E. azurea* was only the fifth most frequent.

Neiff (1986) describes the different types of aquatic vegetation associated with the Paraná River. Seven types of vegetation are separated according to the type and frequency of inundation to which the habitats supporting them are exposed. This author observes that aquatic vegetation is generally less abundant and diverse in the upper stretches of the Paraná River than in the lower stretches well downstream of the study area. Nevertheless, some vegetation types clearly correspond with those observed in the floodplain near Porto Rico. Neiff (1986) includes in his study all kinds of herbaceous species that exhibit requirements for, or tolerance of, at least some degree of inundation. The groups therefore range from those including submerged species to those composed of wetland plants that tolerate water levels below the soil surface for at least part of the year. Some overlap of

species between groups can be expected because aquatic and wetland plants tolerate ranges of hydrological conditions. Four of the seven groups represent the vegetation types that are considered aquatic in this thesis due to their dependence on standing water, although individual species may tolerate periods of low water level. The first of these consists of species belonging to the family Podostemaceae which grow within fast-flowing channels and were not observed in the Porto Rico floodplain. Two other groups represent most of the aquatic vegetation observed. Neiff (1986) associates these with ponds and differentiates them by the frequency with which the river floods the ponds. The first of these is represented by *Myriophyllum aquaticum*, *Eichhornia* spp., *Salvinia* spp. (which also occur in the Porto Rico floodplain), *Nymphoides indica* and *Victoria cruziana*. This group is associated with permanent ponds usually flooded by the river every year. The second type is represented by free-floating species such as *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia* spp. and submerged species such as *Najas marina*, *Ceratophyllum demersum* and *Cabomba australis*. *Eichhornia* spp., *Salvinia* spp., *P. stratiotes*, *M. aquaticum*, *Najas* sp. and *Cabomba* sp. were all observed in the floodplain near Porto Rico but their distribution was not obviously linked to the permanency of ponds, nor even restricted to ponds. The final truly aquatic type includes *Paspalum repens* which was often observed at the edges of the Baía and Ivinheima Rivers but also in lentic areas of water. Neiff (1986) associates this species, together with *Panicum elephantipes*, *P. grumosum* and *Echinochloa polystachya*, with aquatic habitats exposed to low to moderate flow during the high water season. Some of the more amphibious species included in the other vegetation groups also occurred occasionally in the aquatic habitats surveyed, for example, *Polygonum* sp. and *Ludwigia* sp., both wetland plants that have been observed to tolerate water levels ranging from a little below the soil surface to well above it.

The aquatic vegetation types identified during this study generally agreed with those identified by Murphy *et al.* (2003) (Chapter 2, Section 2.4.2). Both studies showed that *Eichhornia azurea* was a major component of more than one vegetation community. In 1999, Murphy *et al.* (2003) observed two different communities in which *E. azurea* was very abundant and a third that was characterised by *Nymphaea amazonum* but with *E. azurea* also present in relatively low abundance. Two communities in which *E. azurea* was dominant were found in 2000-2001. One of these appeared to correspond closely with one of the 1999 groups, while the other appeared to combine features of the remaining two 1999 groups, including the *N. amazonum* group.

In both studies, a high biomass, diverse vegetation community composed of abundant *E. azurea*, together with abundant free-floating species, tended to occur in deep, lotic

waterbodies with low water conductivity and nitrogen-rich sediment. The dominant species tended to be relatively small. A second lower biomass and less species-rich community (represented by two vegetation groups in 1999 and one group in 2000-2001) but with relatively heavy dominant species occurred in slower flowing, shallower water with high water conductivity and nitrogen and phosphorus rich sediments. *E. azurea* tended to be very abundant in this group while free-floating species were less important. The dominance of *E. azurea* was sometimes reduced when *N. amazonum* was present.

The completely submerged, very low biomass community found in 2000-2001 in the fastest flowing, clearest water with low sediment nitrogen and phosphorus was not observed in 1999 because no main channel Paraná sites, where these conditions occurred, were sampled.

Plants that co-occurred and therefore were exposed to the same set of environmental conditions tended to have similar growth forms suited to these conditions. The different vegetation communities identified were therefore characterised by a particular growth form. The distinction of the submerged community from the communities in which free-floating and emergent species were important was particularly marked. This separation according to life form was also found during community analysis of aquatic macrophytes in Itaipu Reservoir, downstream of the study area (Bini *et al.* 1999). The reservoir supports similar species to the floodplain but the distribution and abundance of these differs, with *Egeria najas* dominating the vegetation and *Eichhornia azurea* being uncommon (Bini *et al.* 1999). This contrast illustrates the difference between the two types of river environments but vegetation communities were separated in a similar way. Measurements of water nitrogen, phosphorus, conductivity and pH were in similar ranges in both the reservoir and the floodplain but the environmental characteristics associated with the different communities differed, except for the association of free-floating species with much higher sediment nitrogen and phosphorus than submerged species. Underwater light availability was much greater in the reservoir than in the floodplain, explaining the greater suitability of the reservoir for growth of rooted submerged species. The more constant water level of the Itaipu Reservoir compared to the Upper Paraná floodplain also plays a role in making this a suitable habitat for submerged species. The restriction of submerged species in the Middle Paraná floodplain to isolated waterbodies that are little-affected by fluctuating river levels (Neiff 1986) further illustrates the importance of minimal water level variation for submerged species.

The vegetation of the Paraná floodplain is similar in some ways to the vegetation of the floodplains of other major rivers in South America, including the Amazon and the Orinoco. Like the floodplains of the Paraná River, the Orinoco Delta in Venezuela is affected by upstream dams which have caused reduction in the amplitude of water level variation and now prevent flooding of some areas. The change in water flow has also allowed the daily tides to bring salt water further inland, causing the area of mangroves to increase. As in the Paraná floodplain, topography and the influence of the hydrological cycle vary across the delta. Dry levees support forest formations while depressions may support grasses and sedges or be submerged by temporary and permanent lakes. As the river enters the delta, it divides into several channels, creating a range of flowing water habitats. Analysis of vegetation survey data from the aquatic habitats of the delta by Bertoli (1996) showed two main vegetation types. These were the floating meadows, comprised of species that spend most of their life-cycle in the water surface, and the rooted meadows, comprised of species that can also survive on unflooded soils. Some of the species in the rooted meadow group were encountered during the aquatic plant surveys of the Paraná floodplain but the rooted meadow is generally more comparable with some of the vegetation types observed in the drier B and C sub-sites adjacent to open water. Many of the genera or species in the floating meadow group were also present in the Paraná floodplain. The floating meadow was sub-divided into two groups, the first associated with a variety of lentic habitats that tended to have relatively low pH (3.8–4.9), moderate conductivity ($35\text{--}100\mu\text{Scm}^{-1}$), very low dissolved oxygen levels ($0.1\text{--}1.6\text{mgL}^{-1}$), high water transparency and low water calcium and phosphorus. The second vegetation type was associated with straight, wide, fast-flowing channels where water transparency and conductivity were lower and water pH, dissolved oxygen, calcium and phosphorus were higher. These conditions were not suitable for submerged species intolerant of low light levels and so this group was characterised by *Eichhornia crassipes*, *Salvinia auriculata*, *Paspalum repens*, *Eichhornia azurea* and *Echinochloa polystachya*. The free-floating species were sheltered from the current by the rooted species until they were washed away during floods. The influence of light availability on community assemblage agrees with the results of the Paraná surveys although submerged species did tend to grow in the fastest flowing water because these sites also had the clearest water. The species in the second floating meadow community were observed in channels such as the Baía and Ivinheima Rivers, where the current velocity was moderate, but not in the Paraná where only streamlined submerged species could tolerate the disturbance of the very fast-flowing water.

Environmental factors influencing species distribution

As in the 1999 study conducted by Murphy *et al.* (2003), ordination analysis showed that sediment chemistry variables generally explained species assemblage data better than water chemistry variables. Sediment nitrogen and phosphorus were two of the best explanatory variables in the 2000-2001 data set, while sediment pH and sediment iron were effective in the 2001 data set, and sediment nitrogen and redox potential in the 2000 data set. However, the most effective explanatory variable in this study was water depth. In a study of three lagoons near Porto Rico, Souza, Thomaz & Bini (2002) found that the occurrence and abundance of *Eichhornia azurea* increased with water depth while the occurrence and abundance of *Nymphaea amazonum* and emergent species decreased. In Chapter Two, ordination analysis of the aquatic species data showed that *N. amazonum* was associated with shallow water but the relationship of *E. azurea* with water depth was less clear as it occurred at moderate to high abundance at the majority of sites. However, the results of morphological analysis of *E. azurea* showed that leaf weight, leaf area, stem length and total plant weight increased with water depth, indicating greater success of this species in deeper water. In addition to the water depth preferences of individual species due to their growth form or the conditions that they require to reproduce and germinate, water depth also influences species assemblage indirectly through the effect it has on other environmental conditions, such as water clarity and water nutrient content. The water in shallow lagoons is more easily stirred up by wind than deeper water and also by the activity of benthivorous fish which can reach high densities as lagoons contract and dry up during the dry season. This results in the resuspension of sediment in the water column leading to increased turbidity (King, Robertson & Healy 1997) and also the release of phosphorus from the sediment (Thomaz, Roberto & Bini 1997). The measurement of water depth therefore integrates a number of factors influencing the habitat of aquatic macrophytes.

The selection of environmental predictors of species assemblage was also in agreement with the study of macrophyte distribution in Itaipu Reservoir (Bini *et al.* 1999). Water pH and phosphorus, sediment phosphorus and underwater light attenuation were the best predictors of species assemblage in the reservoir, while the proportion of the water column sufficiently illuminated for plant growth, sediment nitrogen and sediment phosphorus were good predictors in the floodplain. Both studies showed that free-floating species were associated with high water and sediment nutrient levels and submerged species with the clearest water. The importance of sediment phosphorus for free-floating species, although they obtain their nutrition from the water column, can be explained by the process of

phosphorus release from the sediment under anoxic conditions or as a result of turbulence (Bini *et al.* 1999; Wetzel 1983).

Environmental factors associated with variation in species richness and community biomass

There was some agreement on the environmental variables that significantly explained species richness and community biomass between this study and the 1999 floodplain study (Murphy *et al.* 2003). Both studies showed that species richness tended to decrease as sediment calcium and iron content and water conductivity increased. Water depth was an additional predictor in the 2000–2001 data set in contrast with the finding in a study of three lagoons near Porto Rico that species richness was not satisfactorily predicted by water depth (Souza, Thomaz & Bini 2002). Additional variables predicting species richness were also found by Murphy *et al.* (2003). These were water and sediment phosphorus, water alkalinity and three dominant species trait variables. During this study and the study by Murphy *et al.* (2003), these relationships were identified but neither study had the potential to show whether the patterns in species richness or biomass were actually caused by the variation in the variables with which they were associated. The relationships may have been a result of a direct effect of the predictor variables upon the response variables but might also have been caused by the response of both the predictor and response variables to a further unknown variable.

Sediment redox potential and the proportion of the water column able to support photosynthesis were found to be good predictors of community biomass both in this study in 2000 and by Murphy *et al.* (2003). Higher biomass was associated with more oxidising sediment in which levels of nitrate could be expected to be higher and levels of potentially toxic ions lower. Both studies suggest factors influencing the spatial distribution of aquatic vegetation biomass. Biomass may also show temporal variation in relation to the annual flood cycle depending on the species considered. By making monthly measurements of biomass at seven sampling stations during a period of one year, Bini (1996) showed that the biomass of *Eichhornia azurea* was negatively correlated with the river level measured just upstream from Porto Rico. Although the greatest biomass was measured during the period of low river levels, it was explained that this was mainly dead plant material that had accumulated during the growing season because *E. azurea* has a slow decomposition rate following senescence. In contrast, monthly measurements of *Polygonum sp.* biomass made at one location during eight months showed that the biomass of this species was positively correlated with the river level. As a rooted emergent species, the vertical growth

rate had to match the rate of increase in river level in order to keep the photosynthetic structures above water and so biomass accumulation appeared to be closely tied to the flood pulse (Bini 1996). As a free-floating species on the water surface with no need to respond to river level changes, the biomass of *Salvinia auriculata* did not vary during the flood cycle (Bini 1996).

Riparian and floodplain environments

Less research has been conducted into factors controlling the distribution of vegetation associated with drier habitats in the floodplain. Surveys of the floodplain flora around Porto Rico have been conducted and these have recorded 745 species of terrestrial plants (Agostinho, Thomaz & Gomes 2004 in press). Comparison of surveys conducted in different areas of the floodplain suggests that alpha diversity is relatively low but beta diversity is high (Souza, Cislinski & Romagnolo 1997; Agostinho, Thomaz & Hahn 2004).

Because of its rarity following massive deforestation, the gallery forest, occupying elevated banks and levees in the floodplain and islands within the main channel of the Paraná River, has been the subject of most research. Researchers at NUPELIA have used phytosociological approaches to study the forest formations (e.g., Campos, Romagnolo & Souza 2000; Campos & Souza 2002). Therefore, there is information available about the spatial distribution of tree species in riparian habitats but little information about the environmental factors influencing distributions. Campos, Romagnolo & Souza (2000) suggest that the distribution of species categorised by their association with different successional stages confirms the instability of frequently inundated habitats as these habitats support only pioneer and secondary species, while drier habitats support pioneer, secondary and climax species. There do not appear to have been any studies focusing on predominantly herbaceous plant communities in the non-aquatic habitats of the Rio Paraná floodplain.

Two of the vegetation types categorised by Neiff (1986) in his description of aquatic plants of the Paraná system can be recognised as types observed in the Paraná floodplain near Porto Rico. These are the vegetation type associated with seasonally flooded wetlands, characterised by *Polygonum stelligerum*, *P. acuminatum* and *Ludwigia peploides*, and the tall grass swamps that support *Panicum prionitis*, *Andropogon lateralis*, and *Sorghastrum lateralis*. During the surveys of the B and C sub-sites, large areas of vegetation strongly dominated by *Polygonum* were observed, usually at the edges of lagoons where the water table level was close to the soil surface. For example, large, dense areas of *Polygonum* sp.

stretched from the shores of Lagoa dos Patos (Figure 7.1) and Lagoa da Onça well into the floodplain, while the vegetation of the shore and adjacent floodplain area at Lagoa do Jacaré was dominated by *Polygonum stelligerum*. Large areas of dense tall grasses also covered parts of the floodplain, for example, part C of the site BFP on the opposite side of a dry levee from the Baía River. Similar vegetation consisting almost purely of tall grasses was also observed adjacent to Lagoa Ventura, close to the Ivinheima River. The water table was also close to the soil surface at these sites. Both the tall grass and *Polygonum* vegetation types were widely observed in the floodplain in areas of low elevation that appeared to have been undisturbed by human activity.



Figure 7.1 A large area of *Polygonum* sp. stretching from the shore of Lagoa dos Patos into the distance (Claire Dell taking a biomass sample, GU Brazil expedition August 2001).

According to Schessl (1999) the herbaceous plant communities of the Pantanal wetlands have also been little studied. Schessl (1999) reports the species identified during extensive surveys and describes some vegetation types occurring in the north of the Pantanal wetland. In this area, the dry season is much drier than in the Paraná floodplain and different types of herbaceous and scrubby savanna vegetation predominate. During the driest part of the year, some areas are devoid of vegetation. Short tussock grasslands occur in areas that are shallowly flooded by rainwater each year, which is slow to drain away. Sedges and forbs also occur on small mounds created by ants, termites and worms, which are not flooded. Tall tussock grassland occurs where the flooding depth is greater. In lowland areas where the contrast between aquatic and dry phases is most extreme, the

vegetation changes drastically during the hydrological cycle, although some species are adapted to tolerate conditions during both the wet and dry seasons. In addition to these areas that are dry for the greater proportion of the year, some other areas remain flooded all year round, or dry up only briefly. These support floating meadows or wetland areas dominated by *Cyperus giganteus* or *Thalia geniculata*, and in open water communities of aquatic macrophytes. Interspersed with the herbaceous vegetation, different types of scrub vegetation occur, some in habitats elevated above flood levels and some with adaptations that allow them to tolerate seasonal inundation (Schessl 1999).

The Paraná River floodplain shares some characteristics with the floodplain of the Amazon River. However, the hydrological regime vital in structuring the two floodplains differs. In the Paraná River floodplains, the high water season consists of numerous, irregular flood pulses, whereas the annual flood in the Amazon is a much more predictable event with a gradual increase in water level to a single peak flood level followed by a gradual subsidence of water level. Successive plant communities therefore can colonise the same location in the floodplain according to their suitability to the dry phase or the wet phase (Junk & Piedade 1993a). As the dormant period of one community coincides with the growth period of another, primary production in the floodplain may reach very high levels (Junk & Piedade 1993a). The predictability of the flood cycle stimulates the development of adaptations to one phase or the other, or plasticity allowing continued growth as water levels change. For example, free-floating macrophytes are not fixed to a specific growing site and so drift with water movement as water levels rise or fall, and their capacity for rapid vegetative growth allows them to colonise new habitats, even if there are high losses due to stranding and desiccation when water levels drop (Junk 1986). *Eichhornia crassipes* and *Paspalum repens* conserve water during dry spells by reducing the surface area of their leaves, and the leaves of *P. repens* also become more hairy (Junk & Piedade 1993b). *Echinochloa polystachya*, a rooted emergent species, can elongate its stems as water levels rise to keep its photosynthetic structures exposed to the air (Junk 1986). Plants may also adapt to the terrestrial phase by completing their life-cycle very rapidly and producing seeds that can tolerate subsequent inundation, while others may develop aerenchyma in their roots allowing them to tolerate a period of inundation (Junk 1986). Although the hydrological cycle in the Paraná is much less predictable, it is likely that these types of adaptations play an important role in the distribution of species in the floodplain.

7.2.2 Impacts of livestock grazing

The small scale grazing experiments provided simple indications of the earliest stages of regeneration of the vegetation of a relatively elevated bank and a lagoon shore on Mutum Island, following protection from grazing, and of wetland grassland in the Baía floodplain, following cutting. The small plot sizes and short-term duration of the experiments limit the extent to which the results can be used to predict general effects of grazing and patterns in vegetation recovery. There are practical problems associated with setting up enclosure experiments in grazing studies as they reduce the food resource available for livestock and so are costly for the farmer. It may not be possible to create enclosures of a large size or to create replicate enclosures, and the maintenance of such enclosures is likely to be expensive. Some researchers have exploited enclosures originally created for another purpose and so do not have control over their size, location or number. For example, Bock & Bock (1999) compared vegetation cover and bird communities on either side of a fence separating a bird reserve from a cattle ranch. Oba, Vetaas & Stenseth (2001) compared vegetation characteristics between permanently grazed land and seasonally grazed enclosures constructed by livestock farmers as a way of managing their pasture. The duration of the enclosure experiments conducted on Mutum Island was limited partly by the difficulty of managing them from Glasgow but also because more firmly anchored enclosures would have been required if the experiments were to be left in place during the wet season when the river could have flooded the island. However, the positive aspects of the experimental design in the enclosure experiments were the replicated enclosure plots and the similarity of the vegetation in enclosure and adjacent grazed plots at the start of the experiment. Similarly, the cutting experiment also involved replicate cutting treatments arranged in blocks to try to minimize differences in the original vegetation between different treatments.

The reason for conducting the grazing experiments was to ascertain how areas that had been cleared of riparian forest to provide pasture for livestock might begin to recover in the first steps of regeneration of the natural vegetation. In the dynamic floodplain system, patches of vegetation exist in a range of successional states, with succession being reset from time to time by natural flood or fire events or affected by native herbivores. However, the most mature forest vegetation is now rare due to deforestation and so taking steps to restore it, such as preventing livestock grazing, is a major aim in conservation management of the floodplain. In contrast, Verdú, Crespo & Galante (2000) advocate continued grazing as a method of conserving Mediterranean plant and animal communities

in Spain which have been shaped by centuries of grazing. Although fire is a continuing natural disturbance in the area, succession of plant communities towards oak forest has become widespread since grazing disturbance ceased. This has resulted in the loss of open grassland and shrubland habitats which were found to support greater plant and dung beetle species richness and more endemic species (Verdú, Crespo & Galante 2000). The situation in the Paraná floodplain is very different as the vegetation is still semi-natural following a very short grazing history and the natural biotic and environmental disturbances that regulate the system are still more or less in place (although flooding has been reduced). It is therefore desirable from a conservation perspective to allow the vegetation to return to its natural state.

Comparisons of vegetation between grazed sites and ungrazed enclosure sites can be expected to give varying results across different experimental locations and designs, environmental conditions and vegetation community types. However, general trends can be compared if dissimilarities in the experiments are taken into account.

In the Mutum Island enclosure experiments, losses of biomass and canopy height due to grazing exceeded the regeneration capacity of the vegetation and so both of these measurements were lower on open, grazed plots than on enclosure plots. However, the rapid recovery of the floodplain grassland from the cutting treatments showed how infrequent grazing might not have this effect. In the longer running enclosure experiment (experiment two: 132 days), grazed and ungrazed plots differed in species richness and the relative proportions of graminoid and forb species, as well as canopy height and biomass. Both species richness and the graminoid to total biomass ratio were greater in the enclosure plot. As cattle and capybara prefer to consume graminoid species rather than forbs (Quintana, Monge & Malvárez 1998), the change in the relative abundance of graminoid and forb species could suggest that palatable species were increasing, while unpalatable species were decreasing. This suggests that resting the vegetation from grazing improved its quality as a food resource for both livestock and native herbivores. Gabriel *et al.* (1998) also found that palatable species decreased in abundance under moderate and high stocking rates of sheep in Patagonian rangelands while unpalatable species increased. Distel & Bóo (1995) describe different vegetation states in temperate, semi-arid, upland rangelands in Argentina. Transitions between states are stimulated by cattle grazing, together with fire and weather factors. Exclusion of cattle from formerly grazed areas tends to result in an increase in taller grasses of preference to cattle, while these decline and are replaced by shorter but still preferred species if they are exposed to moderate grazing, or by non-preferred species under continuous grazing (Distel & Bóo 1995).

The increased species richness on enclosure plots could be a response to removal of extreme disturbance caused by grazing. This disturbance may have limited species diversity in grazed areas by preventing the growth of all but the species with the best adaptations for tolerating the effects of the livestock. Gabriel *et al.* (1998) also found that grazing reduced species richness in their study of three grazing treatment intensities and an enclosure in Patagonia. Exclusion of sheep from the formerly grazed land caused an increase in species richness during the ten-year course of the experiment, while exposure of the vegetation to a very high stocking rate caused a decrease in species richness. An opposite response was observed by Rambo & Faeth (1999) in their comparisons of areas grazed by cattle, elk and deer with large ungrazed exclosures on Ponderosa pine grassland in Arizona. Species richness was greater in grazed plots. Rambo & Faeth (1999) suggested that grazing reduced competitive dominance of a small number of species and prevented shading by tall canopies, allowing more species to grow successfully.

Both types of response are in agreement with opposite ends of the humpback model of variation in herbaceous species richness with biomass (Grime 1973). In the study by Rambo & Faeth (1999), species richness could be considered limited by competitive dominance, while in the floodplain it could be limited by severe disturbance. Oba, Vetaas & Stenseth (2001) studied variation in species richness with biomass as influenced by cattle grazing on Acacia bush grassland in northern Kenya. Biomass and species richness were measured in continually grazed areas and in seasonally grazed exclosures. Species richness showed a monomodal response to the biomass level, peaking at intermediate biomass resulting from intermediate grazing pressure.

The difference between the vegetation of grazed and ungrazed plots on Mutum Island showed that grazing reduced the diversity and structure of the plant community as well as the overall amount of vegetation. These effects could be expected to have an impact on the floodplain fauna for which the natural vegetation provides habitats and a food resource. The initial transformation from a forest habitat to a grassland habitat when the island vegetation was cleared for grazing is likely to have reduced the capacity of Mutum Island to support animals associated with the riparian forest. This effect was shown by Dobkin, Rich & Pyle (1998) when they compared a forty year old exclosure with a grazed area of riparian meadow in Oregon. In the exclosure, the vegetation was dominated by sedges and forbs characteristic of a wetland habitat, while in the grazed area shrub cover and litter and bare ground were higher, making the site more similar to an upland habitat. The bird community reflected the changes caused by long-term grazing, with the exclosure supporting wetland and riparian birds absent from the open area and the open area

supporting upland birds absent from the exclosure. Bock & Bock (1999) also found effects of grazing on overwintering bird populations in Arizona. They compared the vegetation and bird fauna of an ungrazed bird reserve with an adjacent cattle ranch and found that the lower vegetation height and cover in the grazed area were associated with reduced abundance of ground-feeding, seed-eating birds. The contrasts in vegetation and bird communities were greater during a drought year, suggesting the importance of the role of environmental factors in influencing the impact of grazing. Rambo & Faeth (1999) compared canopy insects between grazed and ungrazed Ponderosa pine grassland sites in Arizona. Although the vegetation differed in species richness and the relative abundances of individual species between the grazed and ungrazed sites, they found that the insect communities were similar. However, the insect abundance was many times lower in the grazed sites.

Although the character of the vegetation on Mutum Island has been changed by deforestation, remnants of riparian forest remain and could act as a source of propagules for regeneration of grazed sites if grazing was stopped. As vegetation is allowed to regenerate in areas where grazing has ceased, it is likely that it will support a greater abundance and diversity of animals, even at the early stages of recovery seen in the exclosure plots.

Livestock numbers on the riverine islands have been reduced since a ban on cattle was introduced to promote regeneration of riparian forest. Much of the formerly grazed vegetation is being given the chance to regenerate under more natural conditions. However, cattle are still permitted elsewhere on the floodplain, for example on the right bank of the Paraná River and on the larger cattle farms on the Baía River. The grazing experiments have suggested that resting cattle fields from grazing could improve the quality of the pasture and at the same time provide more abundant and more diverse vegetation with a greater potential to support some groups of the floodplain fauna.

7.2.3 Competition in free-floating plant communities

Studies of growth rates and of interactions between different species of subtropical, free-floating aquatic plants have been stimulated by the desire to control the weed problems that they sometimes cause and by interest in exploiting their potential for rapid growth to strip nutrients from polluted waterbodies. The results of the competition experiments conducted in the glasshouse can be compared with the results of investigations of the same and other species in monoculture and in competition treatments.

In the *Pistia-Limnobium* experiment, *Pistia* was found to benefit from growth in mixed culture. A similar outcome was observed in a study of the interaction of *Pistia* with *Eichhornia crassipes* in an additive competition experiment of comparable design (Tag El Seed 1978). In this experiment, *Eichhornia* was found to be the dominant species of the pair. Some of the responses of *Eichhornia* to the subordinate *Pistia* were similar to those of *Pistia* when it was grown with the less competitive *Limnobium*. Tag El Seed (1978) found that the yield per plant of *Eichhornia* increased as its density relative to *Pistia* decreased, indicating that intraspecific competition was more important than interspecific competition. This was the response of *Pistia* when mixed with *Limnobium*. Measurement of the variation in specific growth rate of *Pistia* in relation to standing crop density has shown that growth declines as plants become more crowded (Reddy & DeBusk 1984). A rate of 0.18 day^{-1} (doubling time = 3.9 days) was recorded at low plant density but declined to 0.003 day^{-1} at very high density, suggesting the benefit to growth of neighbours of a smaller, lower biomass species (Reddy & DeBusk 1984). Tag El Seed (1978) also showed that mixing *Pistia* and *Eichhornia* caused an increase in the total number of plants produced. A similar benefit of mixing was shown in the *Pistia-Limnobium* experiment as a relative yield total greater than one in fertilised treatments. Agami & Reddy (1990) also showed that the cumulative standing crop of *Eichhornia* and *Pistia* grown in a one to one ratio mixed culture was higher than measurements made for either species in monoculture. In both of the *Pistia* interactions studied, increased availability of nutrients led to increased production of new plants of reduced biomass per plant. This response was also observed by Chadwick & Obeid (1966) as the pH of the growing medium approached the optimum value for *Pistia* success, pH 4.

Despite being a similar size and shape to *Limnobium*, *Salvinia* was much more successful in mixed culture with *Pistia*, although when in direct competition with *Limnobium*, its growth was slightly suppressed. The good competitive ability of the *Salvinia* genus is shown by the dominance of *Salvinia minima* over two other small floating species, *Azolla caroliniana* and *Spirodela punctata*, in experimental conditions in a swamp in Florida (Dickinson & Miller 1998). *S. minima* is very similar to *S. auriculata*, except for its smaller size. In experimental enclosures, the three species were grown in monoculture and in mixed culture in an additive design. In monoculture, *S. minima* had the greatest relative rate of spread in summer and in mixed culture reduced the relative rate of spread of either or both of the other two species in summer and autumn. Dickinson & Miller (1998) showed that *S. minima* was the most buoyant of the three species and suggested that this, together with its larger size and greater height above the water surface, may have contributed to its success in competitive conditions. Although they studied the growth of

Salvinia auriculata only in monoculture, Coelho, Lopes & Sperber (2000) showed that the morphology of this species changes in response to crowding with an increase in the length and area of floating leaves, which become folded and upright, and in the length of submerged leaves. This plasticity, together with the formation of layers of plants, explains how *Salvinia* biomass, yield per initial plant and biomass per unit area could be greater in fertilised than unfertilised treatments in the *Pistia-Salvinia* experiment without a corresponding increase in percentage cover. Like *Pistia*, the relative growth rate of *Salvinia molesta* (synonym *S. auriculata*) (Sale *et al.* 1985) declines with crowding, but the transition to a more compact, space-saving form of greater leaf surface area and the formation of a thick mat of layers of plants may have helped it to resist competitive suppression by the larger *Pistia* plants.

In the study of interaction between *Salvinia* and *Limnobium*, *Salvinia* might have been expected to dominate *Limnobium* because it appeared to match the competitive ability of *Pistia*. However, *Limnobium* showed increased yields per plant and per unit area in response to mixing with *Salvinia* while values for these variables were similar for *Salvinia* in each competition treatment. Agami & Reddy (1989) also reported a lack of effect of mixing with *Spirodela polyrhiza* on biomass yields of *Salvinia rotundifolia* (synonym *S. auriculata*), which were similar in monoculture and in mixture, although in this case, *Salvinia* had a negative effect on *S. polyrhiza*. In fertilised treatments, the combined yield per plant of *Salvinia* and *Limnobium* was enhanced by mixing relative to monocultures and *Limnobium* showed some aggressivity towards *Salvinia*. As in the *Pistia-Limnobium* experiment where *Pistia* benefited from mixing, the effect of interaction appeared to be a positive one for *Limnobium* and a relatively neutral one for *Salvinia*. The response of *Salvinia* to crowding in this species combination may not have been advantageous because *Limnobium* can produce elongated petioles that hold the leaf blade up in the air rather than allowing it to sit on the water surface. This could have improved light capture by *Limnobium* while shading *Salvinia*. The presence of *Salvinia* may have stimulated this change to a more efficient growth form and also provided physical support for the more upright plants. This type of mechanism has been suggested for the increase in total standing crop seen in mixed culture of *Hydrocotyle umbellata* and *Eichhornia crassipes* relative to monocultures (Agami & Reddy 1991). In addition, *Limnobium* also produces long roots, which may have given it an advantage over *Salvinia* in obtaining nutrients from the water, but root characteristics were not measured in the experiment.

The types of responses seen in the competition experiments are in agreement with those found in previous studies.

7.2.4 Role of macrophytes in aquatic food webs

Previous studies of carbon flow in tropical floodplains using stable isotopes have suggested that aquatic macrophytes contribute little to aquatic foodwebs (Lewis *et al.* 2001, Araujo-Lima *et al.* 1986, Bunn & Boon 1993, Hamilton, Lewis & Sippel 1992). As part of this thesis, the possibility that macrophyte carbon might enter aquatic foodwebs through a detrital pathway was investigated. The stable isotope study of macrophytes and sediment in the Paraná floodplain showed that some species were isotopically distinct from each other and from terrestrial vegetation. However, these isotopic signals were not traced successfully into underlying sediment, preventing the investigation of whether invertebrates associated with the sediment were consuming macrophyte derived carbon.

Plant carbon

The $\delta^{13}\text{C}$ results for the *Eichhornia azurea*, *Eichhornia crassipes* and *Polygonum* sp. samples were similar to those usually quoted for C_3 terrestrial plants (-28‰ ; Peterson & Fry 1987), which was expected because the leaves of each of these species are above water where atmospheric CO_2 is available to be fixed in the C_3 pathway. The contrasting photosynthetic mechanism that operates in *P. repens* explains the much less negative $\delta^{13}\text{C}$ value observed in this species. There was no obvious reason for the differences in *P. repens* $\delta^{13}\text{C}$ between the two sites where it was collected. $\delta^{13}\text{C}$ of plants using atmospheric carbon may be lower than expected if ^{13}C depleted CO_2 released during plant respiration or organic matter decomposition dilutes the otherwise more enriched local CO_2 supply available for photosynthesis (Osmond *et al.* 1981). Martinelli *et al.* (1991) have suggested that decreasing $\delta^{13}\text{C}$ of C_4 *Echinochloa polystachya* along the course of the Amazon can be explained by increasing levels of biogenic CO_2 generation downriver.

Adaptations of the submerged species to underwater photosynthesis appeared to result in less isotopic discrimination of carbon than aerial C_3 photosynthesis, but greater discrimination than aerial C_4 photosynthesis. Both *Egeria najas* and *Potamogeton pusillus* have SAM adaptations, including the capacity to fix carbon from bicarbonate ions. When in equilibrium in water with CO_2 , HCO_3^- ions have a $\delta^{13}\text{C}$ value which is about 8‰ more enriched than CO_2 (Osmond *et al.* 1981). Plants utilising this source of carbon therefore can be expected to show a greater enrichment in ^{13}C than those exploiting only dissolved CO_2 . Although *P. pusillus* and *E. najas* can both fix HCO_3^- , the noticeably less depleted

$\delta^{13}\text{C}$ of *P. pusillus* suggests that the photosynthetic strategies are not exactly the same, leading to differences in the degree of fractionation.

Charophytes obtain their carbon from dissolved CO_2 and fix this by C_3 photosynthesis. With both carbon source and photosynthetic mechanism differing from the other two submerged plants, this species also had a contrasting isotopic composition, which was almost as depleted in ^{13}C as the species with aerial leaves.

Carbon isotope analysis of a selection of aquatic plant species common in the Paraná floodplain has shown that species exploiting different carbon sources and with different photosynthetic physiology have contrasting and distinctive carbon isotope compositions. *P. repens* was the species most enriched in ^{13}C , followed by *P. pusillus*, then *E. najas* and submerged epiphytes, while the floating and emergent species with aerial leaves, *E. azurea*, *E. crassipes* and *Polygonum* sp., were the most depleted. The $\delta^{13}\text{C}$ values of *P. repens*, *P. pusillus*, *E. najas* and attached algae differ markedly from the $\delta^{13}\text{C}$ values associated with phytoplankton (-32.4‰ in the Paraná, -35.6‰ in the Baía; Lopes 2001) and the C_3 macrophytes which tend to be most abundant in the floodplain (-28.1 to -28.9‰; Lopes 2001), suggesting that it may be possible to trace these species if they are assimilated.

Plant nitrogen

A major problem of using $\delta^{15}\text{N}$ to estimate trophic level is illustrated by the difference in $\delta^{15}\text{N}$ values of *E. najas* samples collected from the Paraná channel (mean = 5.9‰, standard deviation = 0.41) compared with samples collected from Pau Veio backwater (mean = 8.1‰, standard deviation = 0.71). $\delta^{15}\text{N}$ can vary substantially according to spatial variation in nitrogen sources and levels of availability. Such variation has the potential to confuse estimates of trophic levels made for consumers because an increase in $\delta^{15}\text{N}$ of around 3‰ (Vander Zanden 2001) may indicate a one level rise in trophic position. There was a similar contrast in $\delta^{15}\text{N}$ between the two samples of *E. azurea* collected from different sites. Boon & Bunn (1994) demonstrate the temporal and spatial variations in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of aquatic macrophytes growing in Australian billabongs and discuss the problems these pose in food web analysis. *Vallisneria gigantea*, *Myriophyllum* sp., and *Ludwigia peploides* varied in $\delta^{15}\text{N}$ between three billabongs by 8, 9 and 10‰ respectively. Seasonal variation in submerged macrophytes was also observed as enrichment in ^{15}N in spring. Forsberg *et al.* (1993) did not refer to $\delta^{15}\text{N}$ in their study of the carbon sources of

Amazonian fish but instead used the results of studies on feeding behaviour available in the literature to assign trophic levels.

$\delta^{15}\text{N}$ can also differ between plant tissues and with plant age (Handley & Scrimgeour 1997). Variation in $\delta^{15}\text{N}$ according to the age of plant tissues is suggested by the differences between values obtained from live plant tissue and dead plant tissue collected from the same species at the same site. However, the direction of change was not consistent.

The difference in $\delta^{15}\text{N}$ measured in emergent compared to submerged species could be an indicator of different nitrogen sources or acquisition mechanisms. The spatial arrangement of root structures in the emergent plants and the rooted submerged plants suggests that these all have physical access to nitrogen resources in both the sediment and the water column. The contrast in $\delta^{15}\text{N}$ is therefore more likely to be due to differences in the way in which the submerged and emergent plants take up and assimilate nitrogen, rather than in the source. However, all of the submerged plants were collected from the Paraná channel, or waterbodies that are linked to the Paraná at least occasionally. The contrasting $\delta^{15}\text{N}$ could therefore be due to spatial differences in nitrogen sources in the floodplain, although some emergent samples were also collected from waterbodies associated with the Paraná. Further sampling could allow $\delta^{15}\text{N}$ to be compared between different species in the same location, and the same species in different locations, in order to further investigate this potential pattern.

These results show that more samples would be required to allow a confident estimate of producer $\delta^{15}\text{N}$ to be made for each species at each site. They also emphasise the importance of measuring local $\delta^{15}\text{N}$ values in any particular study and not assuming that the same values can be expected for a particular species growing in different locations.

Sediment carbon

Most sites did not show a strong relationship between $\delta^{13}\text{C}$ of leaf material collected from plant stands and $\delta^{13}\text{C}$ of the underlying sediment, or sediment in nearby open water. In fact, the most ^{13}C depleted sediments were collected from underneath the most ^{13}C enriched plant species, *P. repens*. This was a surprising result because, even if carbon was being mixed within the site, it might be expected that the influence of *P. repens* would enrich the sediment with ^{13}C . However, *P. repens* was usually observed growing in

flowing water and so dead plant material may have been removed quickly by the current. Underlying sediments may have been showing the isotopic composition of various upstream carbon sources, rather than local sources. In Pau Veio backwater, which was isolated from the river due to particularly low river levels, sediment carbon was also more ^{13}C depleted than plant carbon. There was no current in this water body and so the depleted $\delta^{13}\text{C}$ of the sediment may have been due to the mixing of *E. najas* carbon with inputs from C_3 leaf litter from surrounding riparian forest, *E. azurea* which was also present, and phytoplankton.

$\delta^{13}\text{C}$ of the sediment in which *E. najas* and *P. pusillus* were rooted in the Paraná channel implied a significant contribution of carbon from these plants. If carbon inputs were entirely from phytoplankton, C_3 macrophytes with aerial leaves or terrestrial C_3 plants (-32‰, -29‰ and -30‰ respectively in the Paraná floodplain; Lopes 2001), a much more depleted sediment $\delta^{13}\text{C}$ value would be expected. Phytoplankton is often cited as the principal food source for invertebrate consumers, with little of their carbon uptake presumed to be from macrophytes (Araujo-Lima *et al.* 1986; Hamilton, Lewis & Sippel 1992). If this is the case for invertebrates living in the Paraná channel site, then they can be expected to have a very depleted $\delta^{13}\text{C}$. However, a more enriched value would suggest that the submerged macrophytes (and possibly attached algae) are providing an important energy source. The enriched sediment $\delta^{13}\text{C}$ value and the absence of any emergent macrophytes that could be an additional source of ^{13}C depleted carbon suggest that this could be a useful site for tracing plant carbon.

Sediment $\delta^{13}\text{C}$ at the Paraná channel site was less negative than each of the potential carbon sources, except for the submerged macrophytes, suggesting that these make a relevant contribution to sediment carbon, although this may or may not be consumed. This was shown by the high percentage contributions calculated from a mixing model. Even when the least depleted alternative source of carbon was considered (C_3 macrophytes), submerged plants and algae were found to contribute more than half of the carbon to the sediment. These results suggest that a significant quantity of submerged plant carbon is available to consumers in the sediment. Any detritivorous animals feeding within this sediment therefore must either assimilate submerged plant carbon or selectively avoid consuming or digesting it.

7.3 Conservation of the Paraná River floodplain

7.3.1 *The need for conservation*

Conservation of the floodplains of the Paraná River between Porto Primavera dam and Itaipu Reservoir is of vital importance because of their rarity, their biological diversity and the continued threats to their survival.

The floodplains represent the last remnant of a once extensive collection of habitats that has been destroyed along the rest of the Brazilian stretch of the river by the construction of large dams. This area now provides a refuge for plants and animals that would formerly have been much more widespread. It is particularly important in providing spawning grounds and nurseries for the fish community which depends upon the availability of sheltered floodplain environments for reproduction.

The enormous diversity of plants and animals supported by the floodplains is due to their high spatial and temporal environmental variability which creates multiple habitat types. Considering the devastation of natural forest vegetation across the rest of Paraná state, this function is of major importance.

River regulation can be considered the largest scale threat to the floodplains and the plant and animal communities that they support, due to the fundamental role that the natural hydrological cycle plays in floodplain functioning. This could have a wide range of consequences, including a reduction in connectivity and therefore exchange of nutrients, organisms and plant propagules between waterbodies; a reduction in the inundated area available for fish spawning and to provide nurseries for fry; alteration in the extent of vegetation communities with different water level requirements; changed rates and patterns of nutrient cycling in the floodplain; and alteration in the processes of erosion and sediment deposition in the main Paraná channel, due to retention of sediment behind dams. Further pressures include livestock grazing, fires associated with the harvesting of Brazilian ginseng, sand and clay extraction from the main channel of the Paraná River and overfishing. The developing leisure industry in the area could also pose a threat to the floodplain as the numbers of visitors and boats increase.

Although the floodplain represents a rare, threatened habitat of importance for its high biodiversity, it also provides a home for a human population and a potential economic resource in a poor area. However, unregulated exploitation of the area in the past has led

to a decline in fish populations through habitat loss and overfishing so that the area now supports very few fishermen. Restoration and careful management of the floodplain, leading to an increase in the fishery resource, therefore could have both conservation and economic benefits.

7.3.2 Protection of the floodplain

Recognition of the value of the floodplains of the Paraná River in Brazil, in terms of their capacity to support high biological diversity, their cultural importance and their beauty, is not a recent development. In 1961, Sete Quedas National Park was created, covering 144 000 hectares from the Ivaí River down to the Sete Quedas waterfalls. However, the protected status of this area was terminated in 1983 when plans for the Itaipu hydroelectric scheme were initiated and the Sete Quedas falls were subsequently submerged by Itaipu Reservoir. The impacts of hydroelectric schemes in Paraná state, the loss of the Sete Quedas waterfalls and the threat of a new dam at Ilha Grande stimulated proposals for new conservation areas. By 1997, a system of Areas of Environmental Protection and Ilha Grande National Park had been designated.

The protected status of the last remaining stretch of semi-natural floodplain on the Paraná River in Brazil indicates state and national recognition of the importance of this area for conservation. All of the study area is within the Area of Environmental Protection of the Islands and Várzeas of the Paraná River. Most of the sites surveyed within the floodplain on the right bank of the Paraná are within the Ivinheima River State Park and most of the islands are included in Ilha Grande National Park. The aims of management of the conservation units are to protect and rehabilitate the natural environments while working to improve the quality of life for the local population and finding sustainable ways to utilise the floodplain resources. Priorities include control of the types of land uses and commercial activities permitted within the conservation units, removal of cattle from islands to allow the vegetation to regenerate, prevention of vegetation clearance by burning, revision of sand and clay extraction licences and continued studies of the biota to ascertain the conservation status of species (Campos 1999b).

Following the designation of Areas of Environmental Protection and Ilha Grande State Park in the 1990s, the next stage in the conservation strategy for the Paraná River is the reinstatement of connectivity between fragmented habitats. This is now being achieved as part of the state-wide Paraná Biodiversity Project, supported by the World Bank through the Global Environment Facility Program. This project aims to conserve the threatened

Brazilian Inland Atlantic Rainforest and Araucaria Forest ecosystems which are globally significant in terms of biological diversity and endemism. The development of a network of biodiversity corridors to link up fragmented habitats throughout Paraná forms an important part of the project. Two of the three major biodiversity corridors are associated with the Brazilian Inland Atlantic Rainforest and one of these stretches from Caiuá in the north west of Paraná state to Ilha Grande, following the course of the Paraná River and including the islands and floodplain of the river. The other links the largest remnant of forest in Iguaçu National Park with the Paraná River and with areas around Itaipu Reservoir. Further secondary corridors extend into the interior of the state. In addition to the implementation of the biodiversity corridors, the project involves rehabilitation of reserves, prohibition of detrimental infrastructure developments, reduction in illegal clearing and burning of vegetation and elimination of cutting of Araucaria forest and harvesting of forest products. These aims are to be achieved by improving cooperation between environmental agencies and land users, increasing training in biodiversity conservation concepts and practices for those involved in implementing the project and in farming the land and by increasing monitoring of conservation units and enforcement of conservation laws.

7.4 Future work

Researchers at the Universidade Estadual de Maringá began their studies of the Paraná floodplain near Porto Rico in 1987 but the size of the system and its environmental and biological diversity mean that there is still an enormous amount of work to be done in order to understand how it functions. The temporal variability of the floodplain as a consequence of the annual variation in river level, and the likelihood that the floodplain is responding to artificial regulation of this pattern, both add further complexity.

In this thesis, an extensive survey approach was taken to try to describe some of the larger scale patterns in the floodplain vegetation across three habitat types defined by their proximity to open water. With more time and resources, it would certainly be desirable to identify the plants encountered during the surveys to species level. The lack of taxonomic resolution proved a problem when trying to classify the vegetation in waterside and terrestrial habitats. These areas were often dominated by grasses, which without flowers could not be identified even by taxonomists familiar with the floodplain vegetation. In combination with measurements of collective vegetation characteristics and dominant species trait variables, more detailed species data would allow more precise analysis of

how the floodplain vegetation responds to the environment and to biotic and anthropogenic factors.

Several relationships were found between vegetation characteristics and the measurements made of soil or sediment and water properties. However, measurements were made at a single point in time, although environmental factors could be expected to vary over time. In contrast, the single measurements made of the vegetation at each site integrate the ranges of environmental conditions occurring at the site over the long term and so single environmental measurements might not be representative of the conditions shaping the vegetation. Repeat measurements of environmental variables over time would be required to identify the typical conditions associated with particular vegetation types. This could improve confidence in relationships found between the vegetation and the environment. Nevertheless, the relationships found in the first two years of this study were applicable to a new data set collected in the third year, showing that the approach of sampling several sites at a wide range of habitat types within a relatively short time scale each year produced reliable results.

The environmental variables measured during the study are influenced by the river hydrological cycle (Thomaz, Roberto & Bini 1997) and so reflect variations in water level and flow, but water levels and flow velocity themselves were not monitored during this study. Categorisation of sampling sites according to whether the water was flowing or not suggested a role of water velocity in determining plant distribution, as could be expected. Free-floating plants and those that were rooted but with floating parts were not observed in the fastest flowing water. By measuring water velocity itself, another source of variation in species distribution and in vegetation physical attributes could be accounted for. Similarly, bank and floodplain vegetation is expected to be affected by the frequency, depth and duration of floods but these factors were not assessed. The association of flood events with terrestrial vegetation decomposition and nutrient cycling suggests that the soil variables measured were influenced by the flood patterns to which each site was exposed. However, monitoring of the susceptibility of particular sites to floods and the depth and duration of these floods could help to explain the vegetation types found at these sites. This would allow the role in structuring plant communities of floods of different duration and frequency to be investigated. Flood-dependent vegetation types could be identified as well as those with no resistance to flooding. This knowledge would contribute to understanding how the vegetation communities can be expected to respond to river regulation, and whether any particular vegetation types would be threatened by reduced flooding.

The grazing experiments constitute a first step in the investigation of the effects of grazing on natural vegetation and the recovery of formerly intensively grazed vegetation following cessation of grazing. Larger scale exclosures on cattle ranches could be used to investigate whether removing or reducing the intensity of grazing pressure would increase the species and structural diversity of the vegetation and its capacity to support other organisms.

Reduced grazing clearly results in a greater quantity of vegetation available for food and shelter for floodplain organisms, but for grazed vegetation to be of value in conserving the floodplain fauna, it would need to provide the correct types of habitats. It would therefore be useful to monitor any changes in invertebrate and other animal groups associated with the vegetation. Considering the need to balance economic factors with conservation in the floodplain, this would help to establish whether the priority for conserving floodplain animals should be partial restoration of large areas of grazing land or encouragement of complete regeneration of forest in smaller areas. The cutting experiment suggested that natural vegetation might be able to support some level of grazing and so the possibility of sustainable grazing in areas of semi-natural vegetation still able to support the native plants and wildlife of the floodplain could be investigated. This would also require research into the palatability to cattle of native vegetation. Such semi-natural areas could also form small-scale corridors linking patches of natural or restored areas, encouraging movement of animals within the floodplain.

In addition to livestock grazing, floodplain vegetation is also at risk from destruction by the fires set by people wishing to collect the root of Brazilian ginseng (*Pfaffia glomerata*) which has commercial value. Large areas of the floodplain may be set alight because this makes it easier to find and dig up the plant, it being one of the earliest species to regrow once the fire has gone out. This practice is not permitted within the protected areas of the floodplain as it is considered detrimental to the vegetation and wildlife, but natural fires most likely play some role in structuring vegetation communities. There may be plant communities that benefit from or rely upon occasional burning. Illegal fires provide an opportunity for surveying the effects of fire on floodplain vegetation, but carefully managed burning experiments would provide control over the intensity of burning, as this is likely to affect the plant response.

The most obvious drawback of the aquatic plant competition study was its artificiality. This work could be extended by conducting experiments within the floodplain both in experimental enclosures and by monitoring species interactions in waterbodies. If experiments were to be conducted in Brazil, species with different growth forms could also be studied by transplanting individuals. This would also allow seasonal variations in plant

interactions to be studied, which could be important because some species, such as *Eichhornia crassipes* and *Pistia stratiotes*, are frost sensitive. Plant losses due to cold weather could strongly influence the relative success of the different species during the following growing season. Floods can also be expected to wash out free-floating plants from some waterbodies and so the rate at which different species can recolonise could determine community structure. Similarly, recolonisation is necessary after the low water season when dried out lagoons are refilled. Studies of these processes could help to explain the role of biotic interactions in structuring communities.

The approach taken in the stable isotope study to attempt to follow carbon transfer into a detrital pathway was not successful but could be modified. The chances of success might be improved by using a more intensive survey method, involving analysis of individual species and the sediment underneath them at multiple sites in which there were few other plants of similar carbon isotope signature and minimal water movement to prevent mixing of carbon sources. By sampling many “replicate” sites with the same species, any relationship between the plant carbon isotope signature and the underlying sediment would be easier to detect. At sites without too much water movement, there would be a greater chance of finding sediment containing detrital material from the stands of aquatic plants. If a contrast could be found between sediment carbon signatures underneath plant stands and outwith plant stands where the influence of macrophyte carbon could be expected to be reduced, then the organisms inhabiting the sediment and potentially consuming plant detritus could be analysed. Even if macrophyte carbon is not consumed by invertebrates in any form, it should be possible to trace it into the river bed. From here, if not assimilated by invertebrates it is possible that it enters a microbial loop as dissolved organic matter. This pathway involves the consumption of dissolved organic carbon by bacteria, which are consumed by ciliates and heterotrophic flagellates, which are in turn consumed by zooplankton, returning the carbon to the traditional food chain including invertebrates and fish (Brönmark and Hansson 1998).

7.5 Conclusions

This final section provides the answers to the questions that were set in Section 1.2 in order to meet the aims of the project.

- What types of dominant vegetation communities can be identified in three habitat zones within the floodplain (aquatic, bank or shore, adjacent floodplain areas)?

Three major community types were identified in the aquatic habitats of the floodplain, one which included *Eichhornia azurea* in mixture with several free-floating and emergent species, a second in which *E. azurea* was strongly dominant, and a third comprised purely of submerged species.

Two strongly contrasting broad vegetation communities were identified at bank and shore environments. *Polygonum* and *Ludwigia* species were important in one group and Poaceae, creepers, woody plants and ferns in the other group. Sub-groups of these communities can also be suggested, but these are less distinctive.

Most of the floodplain sites supported a Poaceae-creeper community type with the remaining sites supporting a community indicated by *Polygonum* species. The Poaceae group was comprised of a number of sub-communities in which the importance of Poaceae relative to other species varied.

- What characteristics of the vegetation (in terms of collective vegetation variables and traits of dominant species), plus associated environmental characteristics, distinguish these communities?

The aquatic vegetation communities were structurally very different, with contrasting community biomass, canopy height, canopy cover, species richness and stem density. They were associated with waterbodies with different water depth and pH and different sediment nitrogen and phosphorus contents. Water flow rate and underwater light availability also differed between the sites that tended to support the different vegetation types. The two major bank and shore vegetation communities differed in canopy cover, in the soil nitrogen, phosphorus and calcium levels with which they were associated and in the steepness of the bank on which they tended to grow. Floodplain vegetation communities contrasted in species richness and differed in the soil nitrogen and calcium levels and river systems with which they were associated.

- Which environmental and dominant species trait variables are effective predictors of collective vegetation characteristics such as community biomass and species richness?

Aquatic species richness was best predicted by a combination of sediment calcium content and canopy height and cover, while biomass was best predicted by the proportion of the water column sufficiently illuminated for plant growth. A small amount of variation in

canopy height was explained by water conductivity and, like canopy cover and stem density, canopy height was also related to other vegetation variables.

There were reasonably strong relationships between bank and shore species richness and soil nitrogen and phosphorus levels. The variation in the remaining collective vegetation variables was not explained by environmental variables, although there were relationships with dominant species trait variables and other collective vegetation variables.

Some of the variation in floodplain species richness was explained by soil nitrogen, while biomass and canopy cover were well predicted by other collective vegetation and dominant species trait variables. Stem density was related to four environmental variables but was best predicted by a combination of distance from the water's edge, canopy cover and the leaf weight of the dominant species.

- What effect does a single occurrence of biomass removal have on the structure of otherwise relatively undisturbed wet grassland vegetation?

The wet grassland vegetation rapidly recovered from cutting so that canopy height, biomass and species richness were similar between partially cut plots, plots cut down to ground level and untreated plots at the end of the experiment. The vegetation has the capacity for rapid regeneration, suggesting some potential for sustainable grazing, but the effects of the continuous biomass removal and trampling caused by livestock require further investigation.

- What effect does the removal of cattle grazing pressure have on the structure of formerly grazed island vegetation?

Vegetation responded to protection from grazing with increased canopy height, species richness, total biomass and proportion of the total biomass comprised of grasses. Reduced grazing therefore could result in an improved habitat for native organisms and a more palatable fodder resource for cattle.

- How is the growth of three species of free-floating aquatic macrophytes affected by competitive interactions and nutrient availability?

The results of the competition experiments supported observations made in the field.

Pistia and *Salvinia* were well matched in competitive ability and showed no aggressivity to

one another. Interaction suppressed combined yield in low nutrient conditions but not in high nutrient conditions. Interaction of *Pistia* with *Limnobium* resulted in increased *Pistia* growth and suppressed *Limnobium* growth. Increased nutrient availability further enhanced *Pistia* growth but did not affect *Limnobium*. In the interaction of *Limnobium* with *Salvinia*, *Salvinia* growth was slightly suppressed, showing that competitive outcomes were specific to the pair of species considered. In both interactions involving *Pistia*, biomass per plant was reduced by high nutrient availability, as these conditions stimulated the production of daughter plants rather than the growth of existing plants. *Limnobium* showed a similar response in interaction with *Salvinia*.

- Do different species of aquatic macrophytes growing in the Paraná floodplain exhibit distinctive stable carbon isotope signatures?

Contrasting carbon isotope signatures were measured in plants utilising four different photosynthetic strategies: emergent C₃ mechanism; emergent C₄ mechanism; submerged HCO₃⁻ users; and submerged C₃ CO₂ users.

- Can stable carbon isotope signatures be used to trace aquatic macrophyte carbon into a detrital food web?

In this case, the approach was not successful because expected contrasts in sediment $\delta^{13}\text{C}$ were not observed. The sampling design could be modified to increase the chance of detecting any flow of carbon from aquatic macrophytes into invertebrate consumers. An alternative pathway of the movement of carbon in macrophyte detritus into a microbial loop, rather than directly into invertebrates, could also be investigated.



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